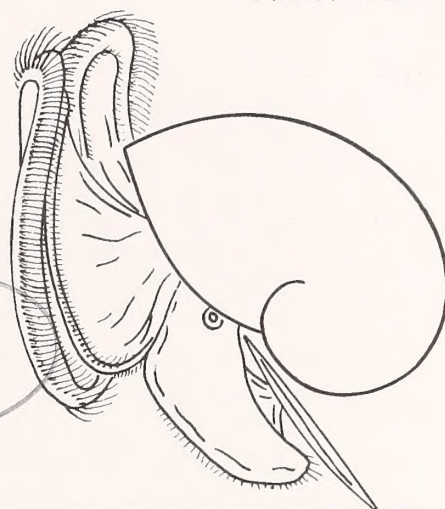
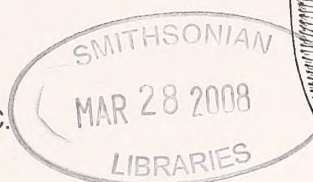




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CONTENTS

Anatomical Review and Preliminary Phylogeny of the Facelinid Nudibranchs (Opisthobranchia: Aeolidina) of the Taxon <i>Phyllodesmium</i> Ehrenberg, 1831 DELISSE M. ORTIZ AND TERRENCE M. GOSLINER	1
Earliest Record of the Genus <i>Haliotis</i> (Mollusca: Gastropoda) from the Late Cretaceous (Campanian) of Los Angeles County, California LINDSEY T. GROVES AND JOHN M. ALDERSON	24
Predatory Behavior and Diet of <i>Eupleura sulcidentata</i> Dall, 1890 (Gastropoda: Muricidae) from West Florida GREGORY S. HERBERT AND SHUBHABRATA PAUL	27
A Large New Species of <i>Lobatus</i> (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with Notes on the Genus BERNARD M. LANDAU, GIJS C. KRONENBERG, AND GREGORY S. HERBERT	31
First Record of the Northeastern Pacific Patellogastropod Genus <i>Acmaea</i> from the Miocene of Japan and Its Paleobiogeographic Implications YUKITO KURIHARA AND TOMOKI KASE	39
A New <i>Phaenomenella</i> Fraussen & Hadorn, 2006 (Gastropoda: Buccinidae), from the Andaman Sea. KOEN FRAUSSEN	48
Development of <i>Tylodina fungina</i> Gabb, 1865 (Gastropoda: Notaspidea) from the Pacific Coast of Panama RACHEL COLLIN	51

CONTENTS — Continued

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THE VELIGER

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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

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Anatomical Review and Preliminary Phylogeny of the Facelinid Nudibranchs (Opisthobranchia: Aeolidina) of the Taxon *Phyllodesmium* Ehrenberg, 1831

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Abstract. The anatomy and morphology of species of *Phyllodesmium* are described for *P. parangatum* Ortiz and Gosliner, 2003, *P. magnum* Rudman, 1991, *P. poindimiei* (Risbec, 1928), *P. hyalinum* (Ehrenberg, 1831), *P. crypticum* Rudman, 1981, *P. serratum* (Baba, 1949), *P. colemani* Rudman, 1991, *P. kabiranum* Baba, 1991, *P. macphersonae* Burn, 1962, *P. briareum* (Bergh, 1896), *P. longicirrum* (Bergh, 1905), *P. pecten* Rudman, 1981, *P. opalescens* Rudman, 1991, *P. horridum* (Macnae, 1954), *P. iriomotense* Baba, 1991 and *P. guamensis* Avila *et al.* A phylogenetic analysis supports the monophyly of *Phyllodesmium*. Species possessing an unbranched digestive tract are most basal, while more derived taxa have a highly ramified digestive tract. More basal species form a grade with symplesiomorphies such as an unbranched digestive tract, jaw with many denticles, absence of zooxanthellae and elongate foot corners. The remaining species have elaborate digestive tracts and have undergone morphological and physiological changes allowing the storage of zooxanthellae in the cerata, for use as a secondary food source. It is evident from this study that morphological changes occurring within *Phyllodesmium* correlate closely with their increased association with symbiotic zooxanthellae. This first parsimony-based phylogenetic study of *Phyllodesmium* largely supports the scenario of morphological evolution first proposed by Rudman (1991).

INTRODUCTION

Within the Aeolidina, the most diverse taxon is the Facelinidae with more than 130 described species. One highly specialized group, species of *Phyllodesmium* Ehrenberg, 1831, has received considerable attention owing to the trophic specialization and evolution of symbiosis of members of this taxon. The facelinid taxon *Phyllodesmium* includes nineteen described species, almost all of which are known to be specialized predators on alcyonarian octocorals restricted to the Indo-Pacific tropics and adjacent temperate regions (Rudman, 1981b; Rudman, 1991; Gosliner *et al.*, 1996; Avila *et al.*, 1998; Ortiz, 2001; Ortiz & Gosliner, 2003; Burghardt & Wägele, 2004; Burghardt & Gosliner, 2006). The fact that most of these species also contain symbiotic zooxanthellae and exhibit a range of variation in the elaboration of digestive gland structures to accommodate this symbiosis, makes them ideal candidates for phylogenetic and comparative biological studies. It needs to be determined if *Phyllodesmium*

represents a monophyletic group and, if this proves to be the case, this particular study can illuminate the nature of the evolution of symbiosis within this particular clade.

Species currently placed in *Phyllodesmium* have been placed in several different genera including *Phestilla* Bergh, 1874, *Cratena* Bergh, 1864, *Hervia* Bergh in Mörch, 1871, *Aeolidia* Cuvier, 1798, *Myrrhine* Bergh, 1905, *Favorinus* Gray, 1850, *Godiva* Macnae, 1954, *Ennoia* Bergh, 1896, *Phyllodesmiopsis* Risso-Dominguez, 1964, and *Babiella* Risso-Dominguez, 1964, reflecting the confusion surrounding the systematics of this group. Rudman (1981, 1991) summarized much of this confusion and the historical review will not be repeated here.

Since the late 1800s, there has been a substantial amount of biological interest and research regarding ecological interactions and symbiosis between the dinoflagellate zooxanthellae *Symbiodinium* Freudenthal, zooxanthellae, and a number of different marine hosts. This literature deals mostly with scler-

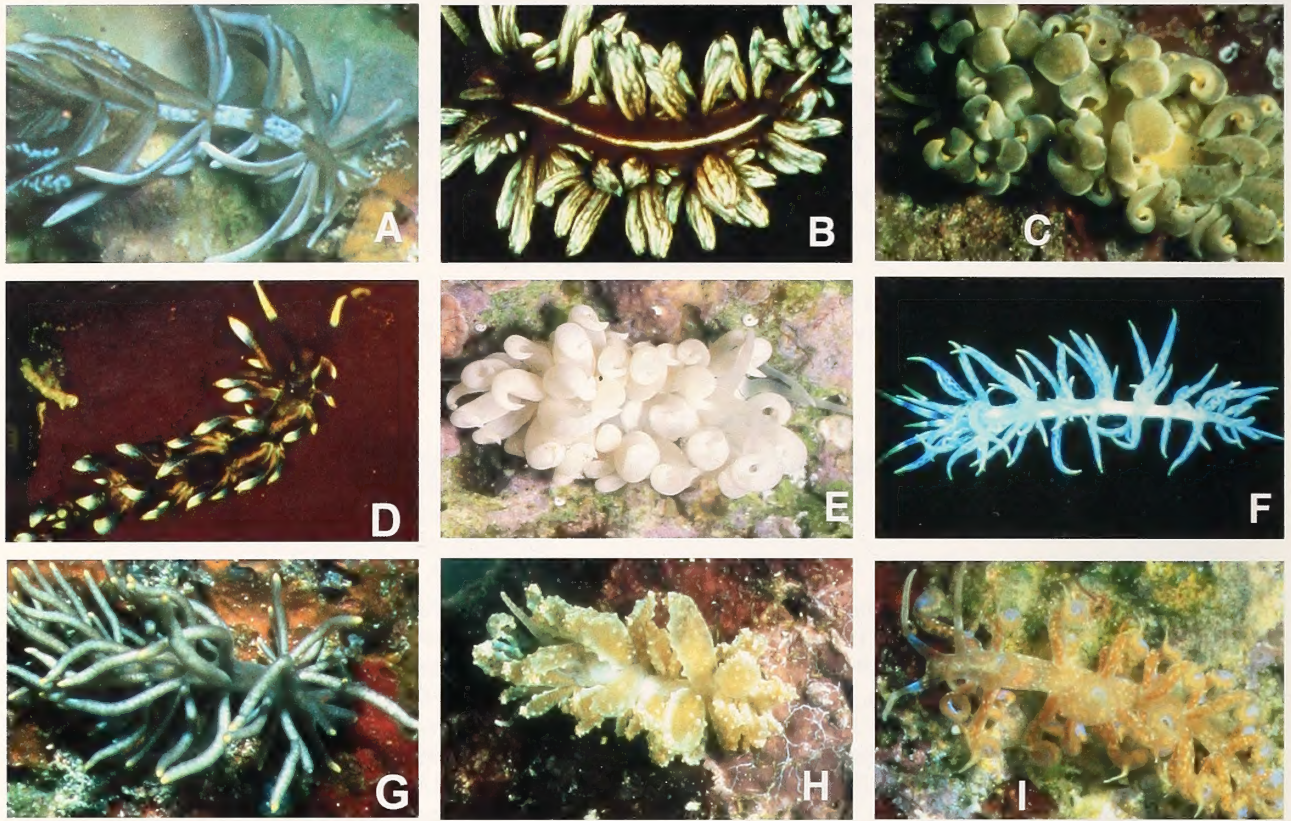


Figure 1. Living animals of *Phylloidesmium* species. **A.** *P. colemani*, photo by T.M. Gosliner. **B.** *P. kabiranum*, photo by R.F. Bolland. **C.** *P. magnum*, photo by T.M. Gosliner. **D.** *P. macphersonae*, photo by R.F. Bolland. **E.** *P. parangatum*, photo by T.M. Gosliner. **F.** *P. serratum*, photo by R.F. Bolland. **G.** *P. briareum*, photo by T.M. Gosliner. **H.** *P. crypticum*, photo by T.M. Gosliner. **I.** *P. poindimiei*, photo by T.M. Gosliner.

actinean corals and species of venerid clams in the taxon *Tridacna* Bruguière (Fankboner, 1971; Goreau *et al.*, 1973; Fitt and Trench, 1981; and many others), but has since expanded into the realm of nudibranch and coelenterate symbiosis. Two examples are Rudman (1982), who worked on the aeolidoidean and arminoidean nudibranch mollusks and Kempf (1984) who studied species of *Melibe* Rang, *Pteraeolidia* Bergh and *Berghia* Trinchese. Hoegh-Guldbergh & Hinde (1986) also examined nudibranch-zooxanthellae symbiosis; they studied the effects of the presence of zooxanthellae on their nudibranch host. Recent works by Burghardt & Wägele (2004, 2006), Burghardt *et al.* (2005), and Burghardt & Gosliner (2006) have examined photosynthetic activity in a variety of additional opisthobranchs, including several species of *Phylloidesmium*.

The available literature, however, has dealt mostly with associations regarding nudibranch and dinoflagellate symbiosis in a descriptive form. Research on the evolution of aeolid nudibranchs and their specific hosts is virtually absent from the literature. Aside

from the work of Rudman (1981a, 1981b, 1982, 1987, 1991), publications regarding evolutionary adaptations as a result of morphological modifications to accommodate the respective symbionts are rare. No phylogenetic study based on the ecological interaction between a facelinid nudibranch taxon and its host has been published. The preliminary phylogeny of the facelinid nudibranchs belonging to the taxon *Phylloidesmium* Ehrenberg, 1831 is the first such study.

The various adaptations and other anatomical variations, which have evolved in species of *Phylloidesmium*, have resulted in it becoming one of the most morphologically diverse in the Aeolidina (Figure 1; Rudman, 1991). The reconstruction of phylogenies within the aeolid nudibranchs has been problematic. Difficulties have been encountered by those systematists that have attempted to clarify the phylogeny of aeolids (Miller, 1974; Gosliner and Ghiselin, 1984). Historically, the branching of the digestive gland, reflected in the ceratal arrangement, and the position of the anus, has been greatly emphasized in the

classification of the Aeolidina (Odhner, 1934). Miller (1971) also considered the "branching of the digestive gland and position of the anus to be main features for delineating genera." The taxon *Phyllodesmium*, as well as its nominal species, have been delineated and described based on these characters. However, Rudman (1991) related ceratal arrangement, digestive gland branching, and other major interspecific morphological characters to the ecology of their food sources.

The purpose of this study is to fully review and supplement the anatomy of species of *Phyllodesmium* in order to produce a preliminary phylogenetic analysis. The results of this study can be used as a basis for examining morphological changes within *Phyllodesmium* in response to coevolution with zooxanthellae symbiosis.

MATERIAL AND METHODS

Morphological Studies

Specimens of previously described species of *Phyllodesmium*, accompanied by color slides of the living animals, were the primary source for morphological characters used in this study. Most importantly, examination of the material housed at the California Academy of Sciences (CASIZ) and the Australian Museum (AM) provided a wealth of specimens that were used to assess and verify doubtful and uncertain characters, as well as developing new characters for the phylogenetic analysis.

Species of Facelinidae were examined and compared morphologically, using reproductive and radular morphology, and anatomical features including ceratal arrangement and structure, location of anus, branching of ceratal digestive gland, and shape of the anterolateral foot corners. Individual specimens were dissected to examine detailed structure of the cerata, buccal mass, and reproductive system. Dissections and scale drawings were made using a dissecting microscope with a camera lucida. An incision was made along the entire midline of the foot. The reproductive systems, as well as external features (e.g., rhinophores, anterior and posterior foot, location of anus, ceratal arrangement, etc.) were then examined.

A LEO series 1400 Scanning Electron Microscope (SEM) at the California Academy of Sciences (CAS) was used to make scaled digital pictures of the structure of the radulae and jaws, in order to survey the phylogenetic characters used in the study. The cerata were dissected and stained. An average of 3 to 4 cerata were extracted from the dorsum of some of the specimens representing several species. Micrographs of the ceratal digestive branching were digitally captured using a Kodak MDS 100 camera

mounted on an M400 Wild microscope. Some of the more problematic cerata were drawn to scale (using a camera lucida on a Nikon SMC-10 dissecting microscope) or photographed (using an FX-35 DX Nikon camera mounted on an SMZ-U Nikon dissecting microscope). The cerata of one species, *Phyllodesmium crypticum*, were stained with a solution of acid fuchsin and 70% ethanol, dehydrated in alcohol, cleared with xylene, and mounted in Permount on a microscope slide.

Phylogenetic Analysis

Taxa. For the phylogenetic analysis, 20 taxa have been considered (Table 1). In order to determine polarity of morphological change within *Phyllodesmium*, specimens of *Godiva quadricolor* (Barnard, 1927) and *Favorinus japonicus* Baba, 1949, were selected as outgroup taxa based on the fact that they represent relatively underived members of the Facelinidae (Willan, 1987). In the absence of a more comprehensive phylogeny of the Facelinidae, we agree with Willan (1987) that these taxa represent appropriate outgroups for polarizing characters within *Phyllodesmium*. These data were compared with the descriptions of *G. quadricolor* from Willan (1987) and *F. japonicus* from Rudman (1980).

Phylogenetic Methods

To develop a phylogenetic hypothesis for *Phyllodesmium*, the morphological data were entered into a data matrix using MacClade 3.01 (Maddison and Maddison, 1992). All the characters used were assigned equal weight and treated as unordered. PAUP 4.0b4a (Swofford, 2000) was used for phylogenetic reconstruction using a heuristic search with the TBR branch swapping option. One hundred random start trees were obtained by stepwise addition. Three characters were deleted in the subsequent analyses due to being uninformative and ambiguous (14, 21 and 30). The deleted characters are indicated in parenthesis in the character description section. Bremer decay analyses were performed by subsequent analysis with a series of iterations that examined successive trees, each one step longer, to estimate branch support using the methodology of Bremer (1994).

Characters. The 31 characters used to resolve the phylogeny of *Phyllodesmium* are listed in Table 2. Of these characters, twenty-nine are binary and two are multistate. The characters states are represented with numbers: 0, "presumed" plesiomorphic condition; 1–2, "presumed" apomorphic conditions (refer to Table 3).

Table 1

Sources used to describe the species in the present study. Abbreviations: R80, (Rudman, 1980); R81b, (Rudman, 1981b); R91, (Rudman, 1991); B37, (Baba, 1937); B91a,b, (Baba, 1991a,b); Bu62, (Burn, 1962); M54, (Macnae, 1954); Rb28, (Risbec, 1928); Be05, (Bergh, 1905); C98, (C. Avila et al., 1998); RC87, (R.C. Willan, 1987); E31 (Ehrenberg, 1831); Br04 (Burghardt et al., 2004); Br06 (Burghardt 2006); T.G., Terrence Gosliner; R.F.B., Robert F. Bolland; PNG, Papua New Guinea; l.r., literature review; p.p., published pictures; p.s., present study; N/A, Non Applicable.

<i>Phyllodesmium</i> species	CASIZ Accesion #	Slide #	Reference	Type of research
<i>P. poindimiei</i>	086009, 93947	T.G.: 086009	Rb28, R91, p.s.	Re-examined
<i>P. parangatum</i>	T.G.: 106472, 105657, 96325, 103702, 105676	T.G.: 105676, 106472, 96325, 105657	p.s.	New Species
<i>P. magnum</i>	79239, 79221	PNG-1988	R91, p.s.	Re-examined
<i>P. hyalinum</i>	69970, 68731	R.F.B 2161	E31, Be05, B37, R81b, R91, M54, p.s.	Re-examined
<i>P. horridum</i>	N/A	p.p.	R81b, R91, M54	l.r.
<i>P. crypticum</i>	99314, 106465	Station 35 Ligo	R81b, R91, p.s.	Re-examined
<i>P. serratum</i>	114759	<i>P. serratum</i> /Okinawa	B91a, R91, p.s.	Re-examined
<i>P. colemani</i>	110358	T.G.: 110358	R91, p.s.	Re-examined
<i>P. kabiranum</i>	89035, 103793	R.F.B. 3158	B91b, p.s.	Re-examined
<i>P. macphersonae</i>	115724, 104700, 65346	R.F.B. 3304	R91, R81b, Bu62, p.s.	Re-examined
<i>P. longicirrum</i>	N/A	p.p.	R81b, R91	l.r.
<i>P. pecten</i>	N/A	p.p.	R81b	l.r.
<i>P. opalescens</i>	N/A	p.p.	R91	l.r.
<i>P. iriometense</i>	N/A	p.p.	B91b	l.r.
<i>P. guamensis</i>	N/A	p.p.	C98	l.r.
<i>P. briareum</i>	65346, 65299, 83678	PNG-1988	R91, p.s.	Re-examined
<i>P. jakobsenae</i>	N/A	p.p.	Br04	l.r.
<i>P. rudmani</i>	N/A	p.p.	Br06	l.r.
<i>G. quadricolor</i>	N/A	p.p.	RC87, B27	l.r.
<i>F. japonicus</i>	N/A	p.p.	R80, B49	l.r.

SYSTEMATIC DESCRIPTIONS

Introductory Remarks

Species descriptions include anatomical information derived from the present study and from literature review. The anatomical data derived from other references have been repeated for a comparison with the data obtained from this study. The data for the re-examined specimens is from original research for the present study, unless otherwise stated in the text. Some morphological characters, such as the distribution and storage of zooxanthellae, could not be determined by the dissections performed, hence literature review was necessary.

Family Facelinidae Bergh, 1889

Phyllodesmium Ehrenberg, 1831

Phyllodesmium Ehrenberg, 1831 [type species by subsequent designation (Gray, 1847), *Phyllodesmium hyalinum* Ehrenberg, 1831]

Myrrhine Bergh, 1905 [type species by monotypy, *Myrrhine longicirra* Bergh, 1905]

Babiella Risso-Dominguez, 1964 [type species by monotypy, *Hervia serrata* Baba, 1964]

Phyllodesmiopsis Risso Dominguez, 1964 [type species by monotypy, *Favorinus horridus* Macnae, 1954]

Diagnosis: Alcyonarian-eating aeolids with cerata capable of being autotomized. Cerata slightly or extremely flattened, lacking functional cnidosacs (a synapomorphy for *Phyllodesmium*). Oral glands absent with a pair of discrete tubular salivary glands present. Rhinophores smooth or slightly nodular (a synapomorphy for *Phyllodesmium*). Foot corners angular (a synapomorphy for *Phyllodesmium*). Ceratal arrangement variable. Pre-cardiac cerata arranged in single or double rows, while the post-cardiac cerata arranged in single or double rowed arches, simple rows, or a mixture of simple row arches and simple rows. Cleioproctic anus present in first post-cardiac arch or behind first postcardiac arch. Masticatory border or jaw with a single row of denticles or smooth (a synapomorphy for *Phyllodesmium*). Radular formula 0.1.0. Teeth usually having long pointed central cusp or reduced one. Each cusp with lateral flange along each side, with or without denticles. Genital opening below anterior limb of first right pre-cardiac arch or row. Reproductive system with single receptaculum seminis.

Table 2
Character descriptions and character states of present study.

1. Body size 0 = moderate 1 = large	12. Anterior foot corners 0 = elongate 1 = angular	23. Radular denticle location 0 = along masticatory border of tooth 1 = extent to central cusp of tooth
2. Branching of digestive gland 0 = absence of branched duct 1 = slightly branched duct 2 = highly branched duct	13. Vertical position of anus on first postcardiac group 0 = posterior 1 = dorsally	24. Base of teeth 0 = long 1 = short
3. Storage of zooxanthellae 0 = absent 1 = present	14. Rhinophore size 0 = long 1 = extended	25. Radular base of teeth 0 = long 1 = short
4. Ceratal surface 0 = smooth 1 = nodular	15. Rhinophore surface 0 = swelling on lamaelle 1 = smooth or slightly nodular	26. Denticle size on jaw plates 0 = small 1 = large
5. Ceratal shape 0 = cylindrical 1 = flattened 2 = smooth	16. Masticatory border of jaw 0 = several rows of denticles 1 = single row of denticles	27. Cnidosac 0 = present 1 = absent
6. Ceratal apex 0 = blunt 1 = curled	17. Number of denticles 0 = numerous 1 = few and elongate	28. Penial spine 0 = present 1 = absent
7. Ceratal arch in precardiac group 0 = present 1 = absent	18. Cusp of teeth 0 = short 1 = long	29. Female gland mass 0 = elongate 1 = bulbous
8. First postcardiac arrangement 0 = arches 1 = rows	19. Radular denticles 0 = present 1 = absent	30. Penial complex 0 = large 1 = small
9. Second postcardiac arrangement 0 = arches 1 = single or double rows	20. Radular denticle arrangement 0 = separated 1 = tightly congested	31. Arrangement of radular denticles 0 = single rows 1 = double rows
10. Third postcardiac arrangement 0 = arches 1 = single or double rows	21. Radular denticle length 0 = long 1 = short	
11. Foot width 0 = wide 1 = narrow	22. Radular denticle tip 0 = blunt 1 = pointed	

Prostate forming gland mass at the base of penis. Penis simple, unarmed.

***Phyllodesmium parangatum* Ortiz & Gosliner, 2003**

(Fig. 1E)

Material examined: Holotype, California Academy of Sciences, CASIZ 106472 near Twin Rocks, Anilao, Batangas Province, Luzon, Philippines, 15 April 1996, T. Gosliner. Paratypes: three specs, one dissected, CASIZ 105657, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 25.3 m depth, 23 February 1995, T. Gosliner. One specimen dissected, CASIZ 105676, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 2.1 m depth, 27 February 1995, T. Gosliner. One specimen, CASIZ 96325, Cemetary Beach, Maricaban Island, Batangas

Province, Luzon, Philippines, 13 March 1994, T. Gosliner.

Distribution: So far, known only from the original localities in the Philippines.

Remarks: The anatomy of this species is completely described by Ortiz and Gosliner (2003).

***Phyllodesmium magnum* Rudman, 1991**

(Figs. 1C, 2A–C)

Phyllodesmium sp. Orr, 1981: 69.

?*Phyllodesmium* sp. Willan and Coleman, 1984: 48, fig. 154.

Phyllodesmium magnum Rudman, 1991: 190–193, figs. 20A, B, 22–24, 27C, D, 28, 29.

Material examined: Two specimens, one dissected, CASIZ 79239, Horseshoe Cliffs, 1 km WNW of Onna

Table 3

Character states present in *Phyllodesmium* species. Data code: see Table 2. Abbreviation: ?, no data available.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>P. horridum</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
<i>P. serratum</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
<i>P. poindimiei</i>	0	1	0	0	0	1	0	1	1	1	1	1	0	0	1	2	1	1
<i>P. opalescens</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>P. briareum</i>	0	2	1	0	0	0	1	1	1	1	1	1	0	1	1	2	?	1
<i>P. colemani</i>	0	2	1	0	1	0	0	1	1	1	1	1	0	1	1	2	?	1
<i>P. magnum</i>	1	2	1	0	1	1	1	1	1	1	0	1	0	1	1	2	?	1
<i>P. hyalinum</i>	0	2	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1
<i>P. crypticum</i>	0	2	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1
<i>P. macphersonae</i>	0	2	1	0	0	1	0	1	1	1	1	1	0	1	1	2	?	1
<i>P. longicirrum</i>	1	2	1	0	1	1	0	1	1	1	0	1	0	1	1	2	?	1
<i>P. pecten</i>	0	2	1	1	1	1	0	0	1	1	0	1	0	0	1	1	1	1
<i>P. iriomotense</i>	0	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0
<i>P. kabiranum</i>	1	2	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1
<i>P. parangatum</i>	1	2	?	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1
<i>P. guamensis</i>	1	2	1	0	1	1	1	1	1	1	0	1	0	1	1	2	?	1
<i>G. quadricolor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>F. japonicus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. jakobseni</i>	1	2	1	0	1	1	?	?	?	?	0	1	0	0	1	1	1	1
<i>P. rudmani</i>	1	2	1	0	0	0	1	1	1	1	0	1	0	0	1	1	1	1

	19	20	21	22	23	24	25	26	27	28	29	30	31
<i>P. horridum</i>	0	1	0	1	0	1	0	0	1	0	?	1	0
<i>P. serratum</i>	0	1	0	1	0	1	1	0	1	0	?	?	0
<i>P. poindimiei</i>	1	1	0	0	0	1	1	1	0	?	1	1	1
<i>P. opalescens</i>	0	0	0	0	0	0	0	0	1	0	1	0	0
<i>P. briareum</i>	0	0	1	1	1	1	0	?	1	0	0	0	0
<i>P. colemani</i>	0	0	1	1	1	1	0	?	1	0	1	0	0
<i>P. magnum</i>	1	1	1	0	1	1	1	?	1	0	1	1	0
<i>P. hyalinum</i>	0	0	1	1	1	0	0	1	1	0	1	0	0
<i>P. crypticum</i>	0	0	1	1	1	1	0	1	1	0	1	1	0
<i>P. macphersonae</i>	0	0	1	0	1	0	0	?	1	0	0	1	0
<i>P. longicirrum</i>	1	1	1	1	1	1	1	?	1	0	1	0	0
<i>P. pecten</i>	0	1	0	1	0	1	1	1	1	0	1	1	0
<i>P. iriomotense</i>	0	0	0	0	0	1	1	1	1	0	?	?	0
<i>P. kabiranum</i>	0	0	1	0	1	1	1	1	1	0	1	0	0
<i>P. parangatum</i>	0	1	0	0	0	1	1	1	1	0	0	0	0
<i>P. guamensis</i>	0	1	1	1	1	1	?	?	1	0	1	1	1
<i>G. quadricolor</i>	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>F. japonicus</i>	0	0	0	0	0	1	0	0	0	0	?	?	0
<i>P. jakobseni</i>	0	1	1	1	1	1	1	1	1	0	0	0	0
<i>P. rudmani</i>	0	1	1	1	1	1	1	1	1	0	0	0	0

Village, Okinawa, Ryukyu Islands, Japan, 1.5 m depth, 6 May 1991, R.F. Bolland. One specimen, dissected, CASIZ 79221, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 6 May 1991, R.F. Bolland.

Distribution: Type locality is New Caledonia, however its distribution is widespread. Northern Western Australia, Marshall Islands and Hong Kong (Rudman, 1991). Collected from Tanzania, Papua New Guinea, Philippines and Japan (Gosliner *et al.*, 1996; present study).

External morphology (Fig. 1C): Body large, broad, up to 120 mm (Rudman, 1991). Present specimens (CASIZ 79239 and CASIZ 79221) 45 mm and 68 mm in length, respectively; elongate body extending broadly from the anterior end, tapering at posterior end. Foot corners, long, angular. Oral tentacles, rhinophores slender, smooth. Cerata large, smooth, flattened and curved apically, extending all along the animal's dorsum. Ceratal arrangement consisting of single vertical rows on distinctive ridges, double row of precardiac cerata along each side of body. Reproductive opening below right-sided double precardiac rows.

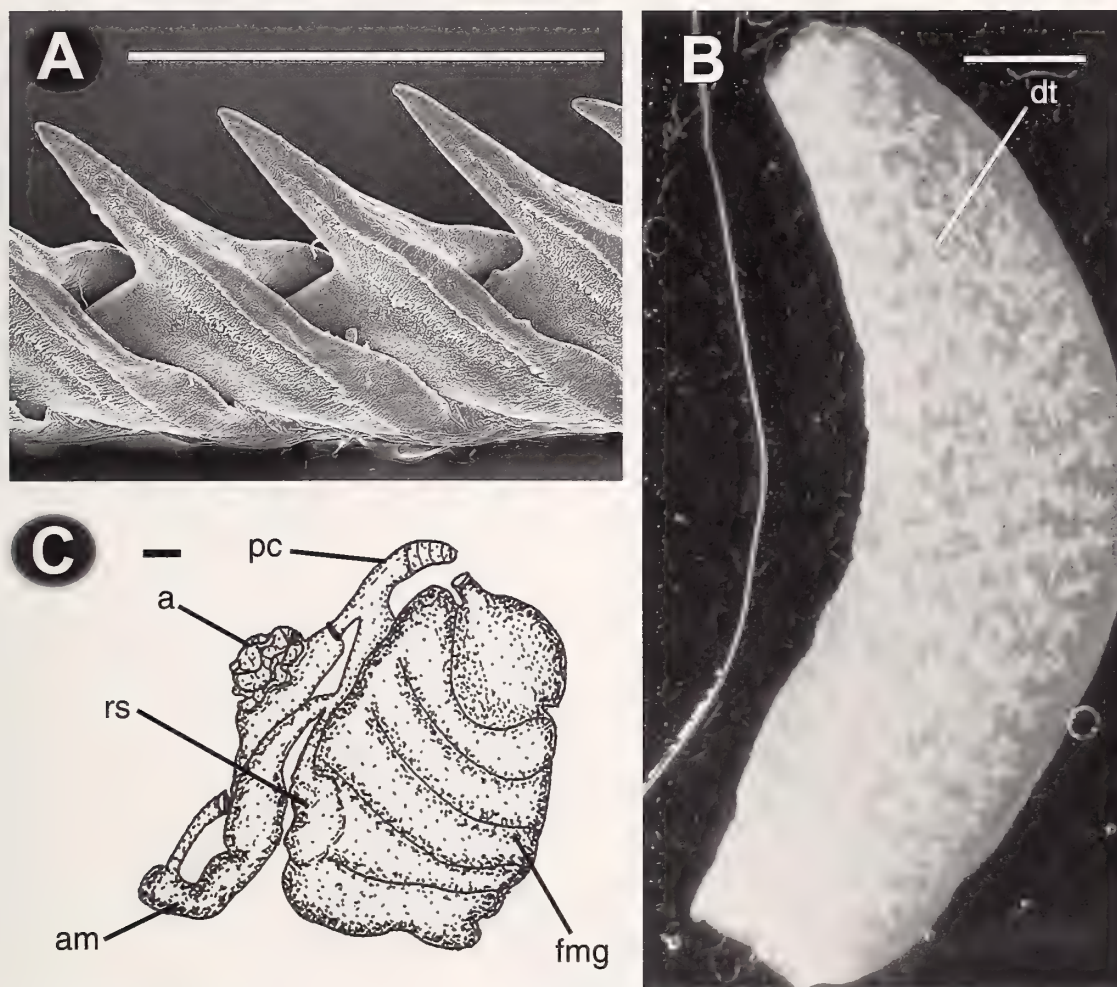


Figure 2. *Phyllodesmium magnum*. **A.** Lateral view of radula. **B.** View of digestive tract in a ceras. **C.** Reproductive System. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.50 mm; **B** = 10 mm; **C** = 5 mm.

Renal opening on right side and centred within interhepatic space. Anal papilla between right postcardiac cerata and behind uppermost cerata of first postcardiac row on prominent mound. Up to 11 postcardiac rows present with up to 8 or more cerata per row.

Cerata and digestive gland (Fig. 2B): Cerata flattened, providing increase of surface area, allowing for the branching of the digestive gland duct on each ceras. Digestive gland extending all along cerata with numerous branches diverging into many secondary and tertiary branches. Flattened branches with terminal chambers; zooxanthellae present in parts of cerata exposed to sunlight, including digestive gland in both the body wall and foot (Rudman, 1991).

Buccal armature (Fig. 2A): Radular formula of 45 mm long specimen $21 \times 0.1.0$ (CASIZ 79239). Tooth short,

with wide base enclosing part of basal posterior structure. Cusp elongate, pointed. Denticles small, short, continuous, extending halfway down each tooth. Jaw with smooth masticatory border (Rudman, 1991).

Reproductive system (Fig. 2C): Preampullary duct long, narrow, extending into a broad, long folded ampulla via thin duct. Duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into short, narrow prostate, connecting to membrane gland via small opening. Prostate with overlying layer of tissue, connecting with a massive, folded and bulbous female gland mass.

Phyllodesmium poindimiei (Risbec, 1928)

(Figs. 11, 3A–C)

?*Phidiana tenuis* Eliot, 1905: 287–288.

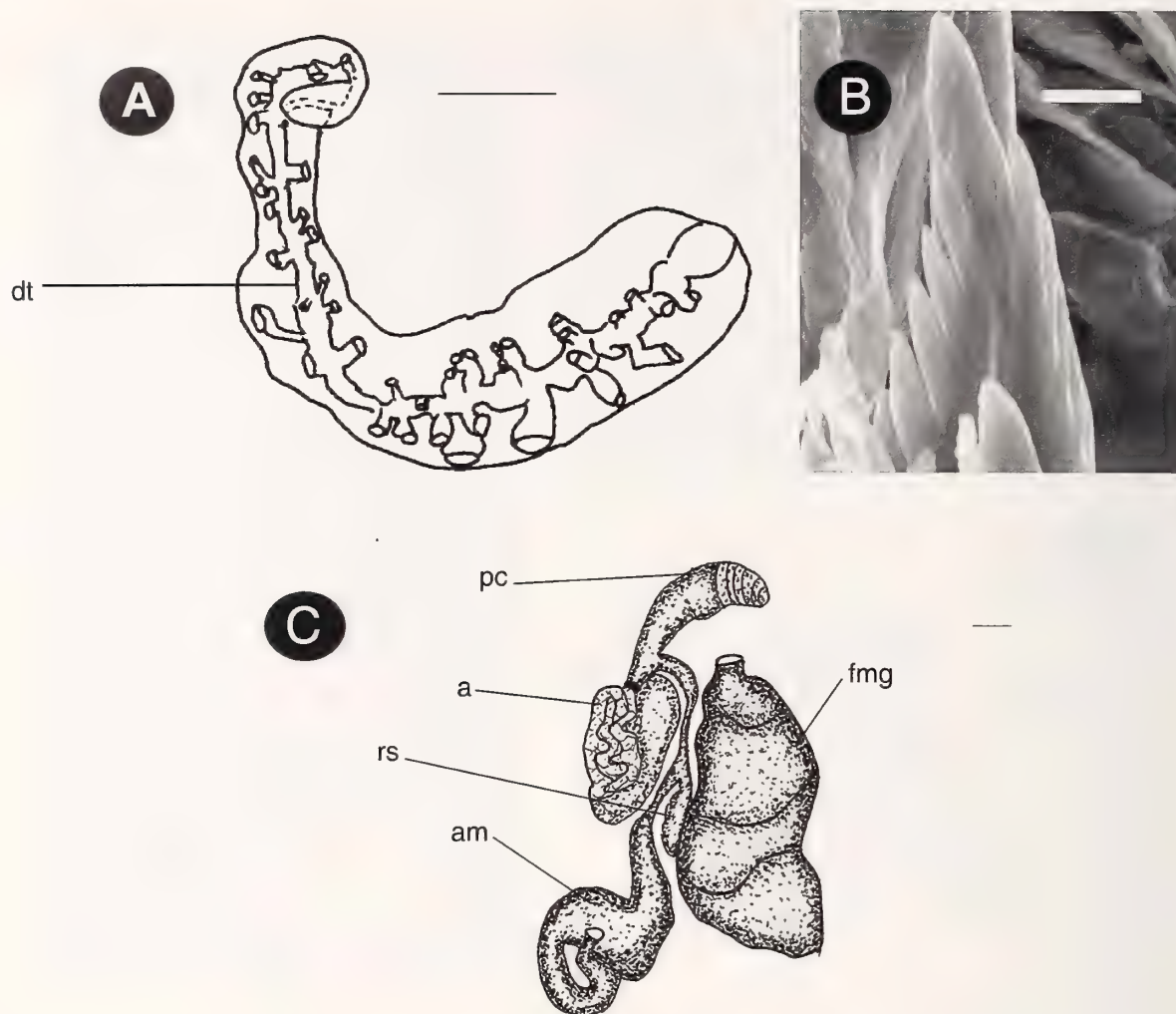


Figure 3. *Phyllodesmium poindimiei*. **A.** View of digestive tract inside a ceras. **B.** Radular denticles. **C.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 10 mm; **B** = 0.002 mm; **C** = 5 mm.

Aeolidia poindimiei Risbec, 1928: 246–247, fig. 78, Pl. 9, fig. 3.

Phestilla poindimiei — Risbec, 1953: 138–139, figs. 93–96.

Phyllodesmium poindimiei — Rudman, 1981b: 224–229, figs. 3–7, 21B, 25C, 27.

Material examined: Three specimens, CASIZ 86009, Devil's Point, NW side of Maricaban Island, Batangas, Luzon Island, Philippines, 25.3 m depth, 26 March 1993, T.M. Gosliner. One specimen, CASIZ 105746, Sepok, Maricaban Island, Batangas Province, Luzon, Philippines, 16.7 m depth, 24 February 1995, T.M. Gosliner. One specimen, dissected, CASIZ 93947, Watubela Islands, E Banda Sea,

Moluccas, Indonesia, 12.1 m depth, 11 November 1993, P. Fiene.

Distribution: Originally described from New Caledonia (Risbec, 1928). Found and redescribed from New South Wales and Western Australia (Rudman, 1991). Specimens also collected from Indonesia, Japan, and the Philippines (present study).

External morphology (Fig. 11): Body of moderate size, elongate, 13.5 mm in length. Body shape wider anteriorly, extending narrowly from anterior to posterior end. Anterior foot narrow anteriorly. Foot corners angular. Rhinophores moderately long, smooth, approximately equal in length size to oral tentacles. Cerata cylindrical, smooth and curved, similar to *P.*

magnum and *P. parangatum*. Dorsum partially exposed, not covered by numerous recurved cerata. Ceratal arrangement, except for the precardiac arch, of single rows with up to 3 to 5 recurved cerata each, on right side of body. Both renal and reproductive openings immediately below precardiac arch, in close proximity to first postcardiac row within interhepatic space. Anal papilla immediately below first postcardiac row. Postcardiac rows ranging from 7 to 9 rows on each side of dorsum.

Cerata and digestive gland (Fig. 3A): Ceratal digestive gland duct extending to apical end of each ceras, branching outwardly in close proximity to ceratal wall. Simple branching ducts perpendicular to central duct, extending in terminal sac in variable manner. Cerata cylindrical, smooth, terminating in curled apex.

Buccal armature (Fig. 3B): Radular formula $24 \times 0.1.0$ (CASIZ 93947). Tooth broad with long base, extending anteriorly and encasing posterior edge of adjacent tooth. Cusp long, with denticulation, extending along centre edge of margin. Degree of separation between elongate, adjacent denticles variable. Masticatory border of jaw smooth (Rudman, 1991).

Reproductive system (Fig. 3C): Preampullary duct long, broad, extending into bulbous ampulla via thin duct. Duct bifurcating into receptaculum seminis and into penial complex. Penial complex extending into large, short, bulbous prostate. Connection between albumen and membrane glands basal. Prostate connecting with folded. Female gland mass long, massive.

Remarks: Rudman (1981) considered the likelihood that *Phidiana tenuis* Eliot, 1905) may be a senior synonym of *Phyllodesmium poindimiei* based on similarities of external morphology and radula. He was reluctant to place these taxa in formal synonymy, pending the collection of additional material from East Africa, the type locality of *P. tenuis*. We concur with this approach to resolving the nomenclature of this species.

Phyllodesmium hyalinum Ehrenberg, 1831

(Fig. 4A–D)

Phyllodesmium hyalinum Ehrenberg, 1831: 32.

Phyllodesmium xeniae Gohar & Aboul-Ela, 1957: 131–144, Pl.1

Favorinus horridus brevitentaculatus Engel and van Eeken, 1962: 28–29, fig. 5.

Phyllodesmium orientale Baba, 1991b:109, figs. 1–3 ; pl. 1, fig. 1, possible synonym.

Material examined: One specimen, CASIZ 69970, Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa, Ryukyu Islands, Japan, 1.5 m depth, 13 May 1989,

R.F. Bolland. Two specimens, one dissected, CASIZ 68731, Hole in the Wall, near Hussein Village, north of Madang, north coast, Papua New Guinea, 6.4 m depth, 21 July 1989, T.M. Gosliner.

Distribution: First described from the Red Sea (Ehrenberg, 1831), but has been recorded more recently from the Philippines (Bergh, 1905), Japan (Baba, 1937), Tanzania (Rudman, 1981b), South Africa (Gosliner, 1987), Papua New Guinea, Japan, Tanzania, Indonesia (present study).

External morphology: Body of moderate size, 10.3 mm in length. Foot wide, extending posteriorly, tapering into reduced posterior end. Oral tentacles long, about equal to the length of smooth rhinophores. Curved cerata numerous, covering surface of dorsum. Ceratal arrangement in arches in precardiac and postcardiac cerata. Number of cerata per arch 7 to 10 on each arch on each side of dorsum. Reproductive opening situated at base of precardiac arch, on right side of dorsum. Renal opening centred in the interhepatic space, in close proximity to first postcardiac arch. Anal papilla on a distinctive mound located on right side of the dorsum, outside arch on the posterior side of the first postcardiac arch. Up to six postcardiac ceratal arches present on each side of the body.

Cerata and digestive gland (Fig. 4C): Digestive gland extending entire length of ceras with secondary and tertiary branches extending in “web-like form” parallel to ceratal wall. Ceratal surface nodular. Branches terminating in small chambers, assumed to be the storage areas for the zooxanthellae from its alcyonacean feeding source, *Xenia* spp. (Rudman, 1991). Nodular cerata flattened and curled apically.

Buccal armature (Figs. 4A–B): Radular formula $25 \times 0.1.0$ (CASIZ 68731). Tooth narrow with long base, elongate cusp. Denticles visible halfway down tooth. Denticles short, pointed, well separated. Jaws with single row of large, sparse denticles all along masticatory border (Rudman, 1991).

Reproductive system (Fig. 4D): Preampullary duct short, expanding into elongate, bulbous ampulla via narrow duct. Duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into large, elongate, folded prostate. Prostate connecting to folded albumen gland, with surrounding membrane gland, and massive and long female gland mass.

Remarks: *Phyllodesmium orientale* Baba, 1991 was described as a distinct species (Baba, 1991b) based on two specimens collected from Japan. Baba noted that it was similar to *P. hyalinum*, except that it has an anal position that is more similar to *P. crypticum*. However,

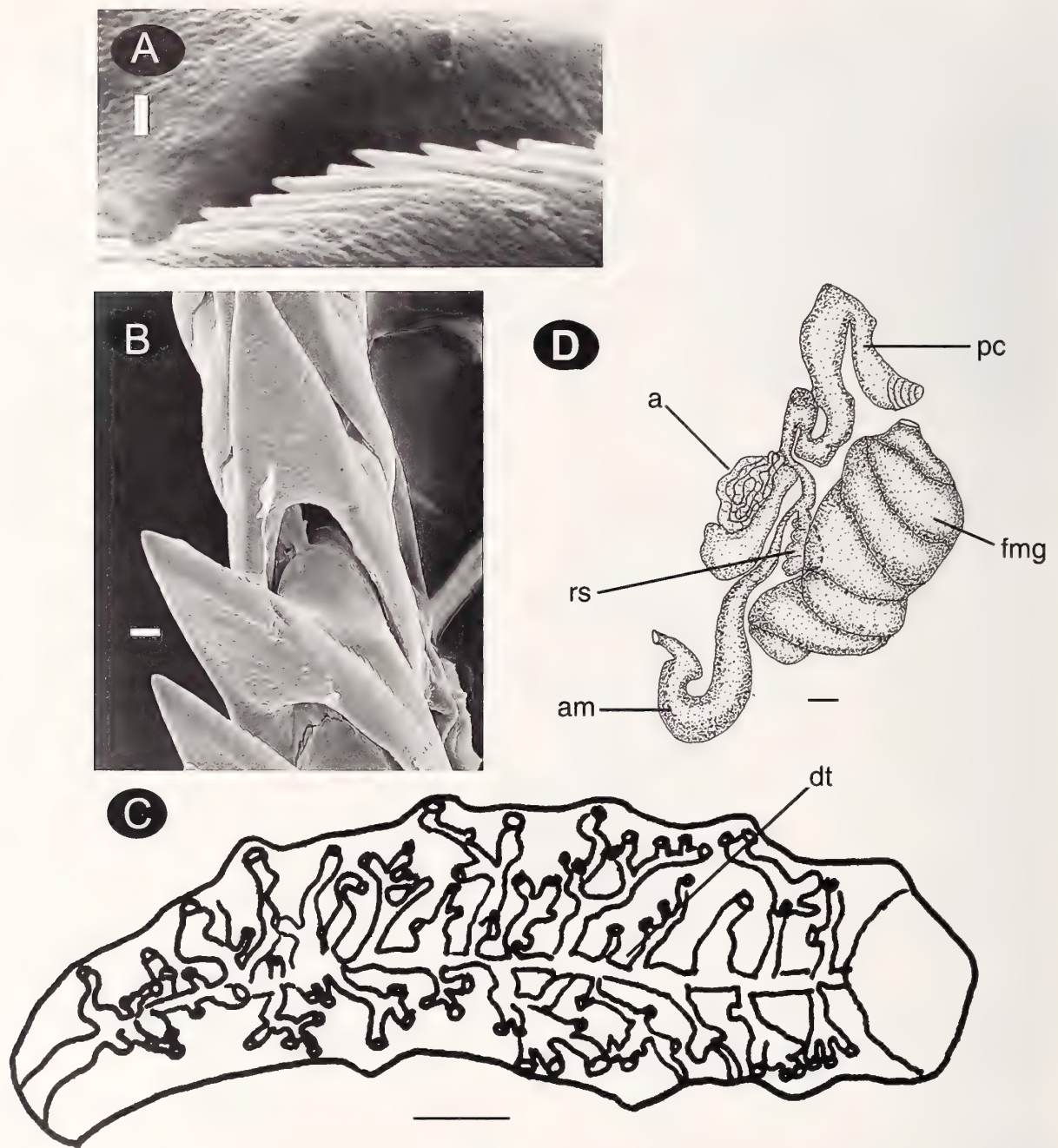


Figure 4. *Phylloidesmium hyalinum*. **A.** Denticles on masticatory border of radula. **B.** Anterior view of radular tooth. **C.** View of digestive tract inside a ceras. **D.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.010 mm; **B** = 0.003 mm; **C** = 5 mm; **D** = 5 mm.

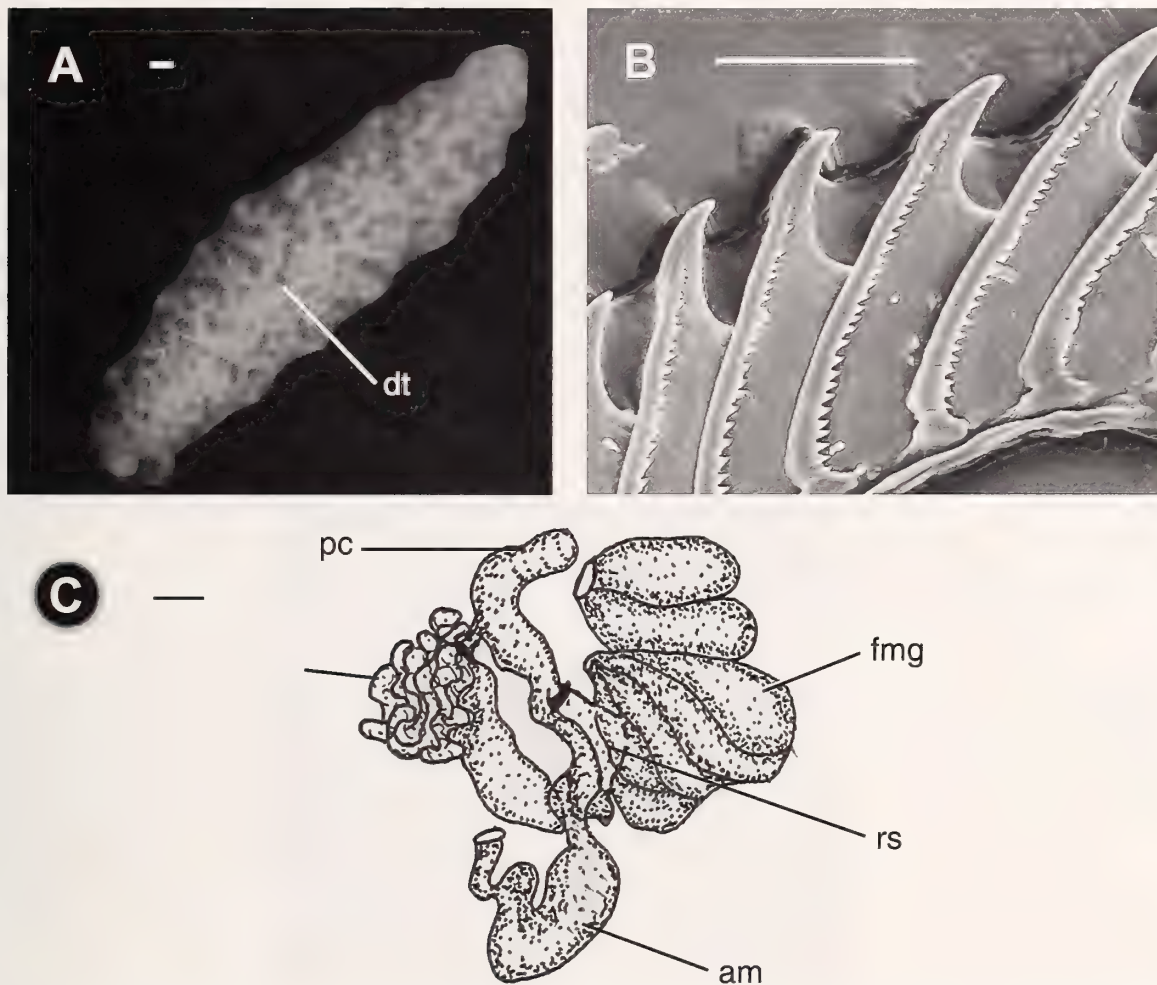


Figure 5. *Phylloidesmium crypticum*. **A.** View of digestive tract inside a ceras. **B.** Lateral view of radula. **C.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 10 mm; **B** = 0.05 mm; **C** = 5 mm.

it is evident from Baba's illustration (pl. 1, fig. 1) that the anus is rather dorsal in its position, similar to *P. hyalinum*. We suspect that *P. orientale* is synonymous with *P. hyalinum* and list it as a probable synonym, pending discovery of more material from Japan.

Phylloidesmium crypticum Rudman, 1981

(Figs. 1H, 5A–C)

Phylloidesmium cryptica Rudman, 1981b: 232–236, 244–261, figs. 10A, B, 11, 12D, 13, 14B, 22B, 23, 26B, 27; Rudman, 1991: 194, fig. 28.

Material examined: One specimen, dissected, CASIZ 99314, Huamja Island, NE side Manua, Mtwara Region, Tanzania, 4 November 1994, T.M. Gosliner. Two specimens, one dissected, CASIZ 106465, near

Twin Rocks, Batangas Province, Luzon, Philippines, 9.1 m depth, 15 April 1996, T.M. Gosliner.

Distribution: Originally described from Dar es Salaam, Tanzania (Rudman, 1981b). Recorded from New South Wales and Western Australia (Rudman, 1991). Specimens collected from Philippines and Japan (present study).

External morphology (Fig. 1H): Body of moderate size, 10 mm in length. Foot wide, elongate, tapered at posterior end. Anterior foot corners tapered. Rhinophores, oral tentacles smooth and long; rhinophores shorter than oral tentacles. Cerata numerous often obscuring dorsum of body. Ceratal arrangement in arches. Number of cerata undetermined due to detachment of most of the cerata of the material examined. Up to 7 postcardiac arches present on each

side of the body. Reproductive opening situated below anteriormost portion of right precardiac arch. Renal opening immediately in front of uppermost portion of the right-sided first postcardiac arch. Anal papilla located within first postcardiac arch, on right side of body.

Cerata and digestive gland (Fig. 5A): Digestive gland extending all along ceras. Ceratal surface nodular with secondary and tertiary branches extending in a "web-like form" to the ceratal wall. Branches terminating in small chambers, assumed to be the storage area for the zooxanthellae extracted from its alcyonacean prey, *Xenia* spp. (Rudman, 1991). Cerata flattened, curved at apex.

Buccal armature (Fig. 5B): Radular formula $24 \times 0.1.0$ (CASIZ 106465). Tooth with broad, elongate base, extending anteriorly to adjacent tooth. Cusp elongate anteriorly. Short, pointed, well-separated denticles present on all teeth. Single row of large denticles present on masticatory border of jaw plates.

Reproductive system (Fig. 5C): Preampullary duct short, extending into long, folded, bulbous ampulla. Ampulla extending via broad duct to receptaculum seminis and penial complex. Penial complex small, with proximal end connecting to massive and folded albumen and membrane glands. Distal end connecting with small, irregular and bulbous female gland mass.

Remarks: *Phyllodesmium hyalinum* and *P. crypticum*, may easily be confused as the same species, but differ in the base of the teeth, anal position, rhinophore size and size of penial complex. *Phyllodesmium hyalinum* has greatly extended rhinophores, an anus located above the first postcardiac arch, a narrow base and a large penial complex. *Phyllodesmium crypticum* has moderately long rhinophores. The anus is inside the first postcardiac arch. The radular teeth have a wide base and the penial complex is small.

Phyllodesmium serratum (Baba, 1949)

(Figs. 1F, 6A–C)

Hervia serrata Baba, 1949: 105–106, 179, pl. 46, figs. 156–157, text figs. 142–143.

Cratena serrata — Baba, 1955: 36, 56.

Babiella serrata — Risso-Dominguez, 1964: 223.

Phyllodesmium serrata — Rudman, 1981b: 260.

Phyllodesmium serratum — Baba, 1991a: 101, figs. A–H: pl. 1 figs. 1–3).

Material examined: One specimen dissected, CASIZ 114759, 1 km WNW of Onna Village, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 44.2 m depth, 18 May 1994, R.F. Bolland.

Distribution: Originally described from Japan (Baba, 1949). Recorded from different regions of Australia: Victoria, New South Wales and parts of the Northern Territory (Rudman, 1991).

External morphology (Fig. 1F): Body, 32 mm in length, moderate size. Foot wide and elongate, tapering posteriorly, tapered anterior foot corners. Rhinophores smooth and moderately long, as long as the oral tentacles. Cerata, smooth, long, straight, extending across whole body, arranged in arches, precardiac arch can have up to five cerata on each side, postcardiac arches range from 7 to 10 arches on each side, each arch containing up to 7 cerata on each arch. Reproductive opening between center and uppermost edge below precardiac arch. Renal opening in front of first postcardiac arch. Anal papilla on a distinctive mound, centred inside first postcardiac arch.

Cerata and digestive gland (Fig. 6A): Branched digestive gland, extending as finger-like projection inside cerata, short lateral branches evident, cerata are cylindrical, smooth, long and numerous.

Buccal armature (Figs. 6B–C): Radular formula $24 \times 0.1.0$ (CASIZ 114759). Tooth wide with short base, extending anteriorly and covering the posterior basal edge of the tooth in front, long cusp, denticulation extending all along border of each tooth. Tightly joined and long denticles, extending into pointed tip, small denticles on masticatory border of jaw plates (Baba, 1991a).

Phyllodesmium colemani Rudman, 1991

(Figs. 1A, 7A–B)

Phyllodesmium sp. Coleman, 1988: 14–15, 1989: 7, 54.

Phyllodesmium colemani Rudman, 1991: 187–190, figs. 14C, 18, 19, 20C–E, 21, 27–29.

Material examined: Two specimens, one dissected, CASIZ 110358, Bus Stop Reef, Balayan Bay, Batangas Province, Luzon Island, Philippines, 23 April 1997, M. Miller.

Distribution: Known from its type locality, Lord Howe Island, Coral Sea (Rudman, 1991) and the Philippines (present study).

External morphology (Fig. 1A): Body 22.5 mm in length, of moderate size, extending uniformly narrowly from anterior to posterior end. Foot narrow and elongate. Rhinophores greatly extended and smooth, similar to oral tentacles. Cerata long, smooth, flattened, extending along dorsum of body, visible dorsum. Ceratal arrangement with single postcardiac vertical rows and precardiac arch, up to 3 to 4 cerata on each of the 7 to 8 postcardiac rows located on each side of body, up to 3 to 5 cerata on each side on precardiac

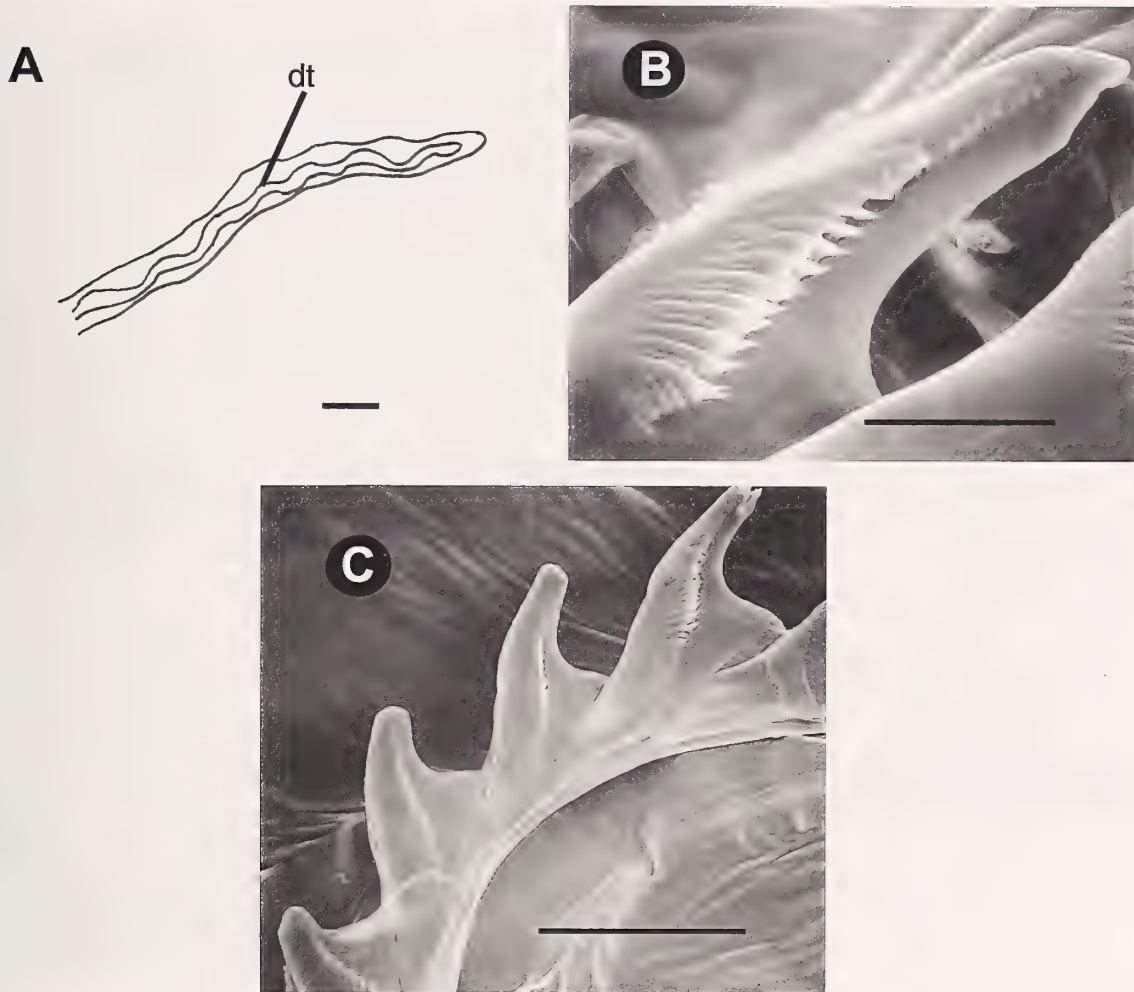


Figure 6. *Phyllodesmium serratum*. **A.** View of digestive tract inside a cerata. **B.** Lateral view of radula and its denticles. **C.** Lateral profile of radula. Abbreviations: dt, digestive tract. Scale bars: **A** = 5 mm; **B** = 0.02 mm; **C** = 0.07 mm.

arch. Reproductive opening, renal opening, and anal papilla located on right side of body. Reproductive opening located below anterior-most portion of pre-cardiac arch, renal opening located in center of interhepatic space; anal papilla raised on a distinctive mound, located outside first postcardiac row.

Cerata and digestive gland (Fig. 7A): Cerata long, slender, flattened, smooth. Ceratal apex blunt. Digestive gland extending all along cerata through central duct; central duct bifurcating into perpendicular secondary branches terminating in bilateral and broad branches. Upon examination of translucent ceratal tissue, the uniformity and extent of the branching is visible.

Buccal armature (Fig. 7B): Radular formula $26 \times 0.1.0$ (CASIZ 110358). Tooth wide and long, base extending anteriorly, covering posterior portion of front tooth. Cusp long and narrow in anterior portion of the tooth. Denticles visible on central part of each tooth, short

and separate from each other, terminates in pointed tip; smooth masticatory border of jaw (Rudman, 1991).

Reproductive system: Reproductive system similar to that described for the other species of *Phyllodesmium*, although, as in *P. opalescens*, the prostate gland is very large (Rudman, 1991).

Phyllodesmium kabiranum Baba, 1991

(Figs. 1B, 8A–D)

?*Eolida bella* Rüppell & Leuckart, 1831: 35, Pl. 1. 10, fig. 4.

?*Phyllodesmium bellum* — O'Donoghue, 1929: 715.

Phyllodesmium kabiranum Baba, 1991b: 113, figs. 4–5, Pl. 1, fig. 2.

Material examined: One specimen, CASIZ 89035, Seragaki Beach, 1.3 km ENE of Maeki-zaki, Okinawa,

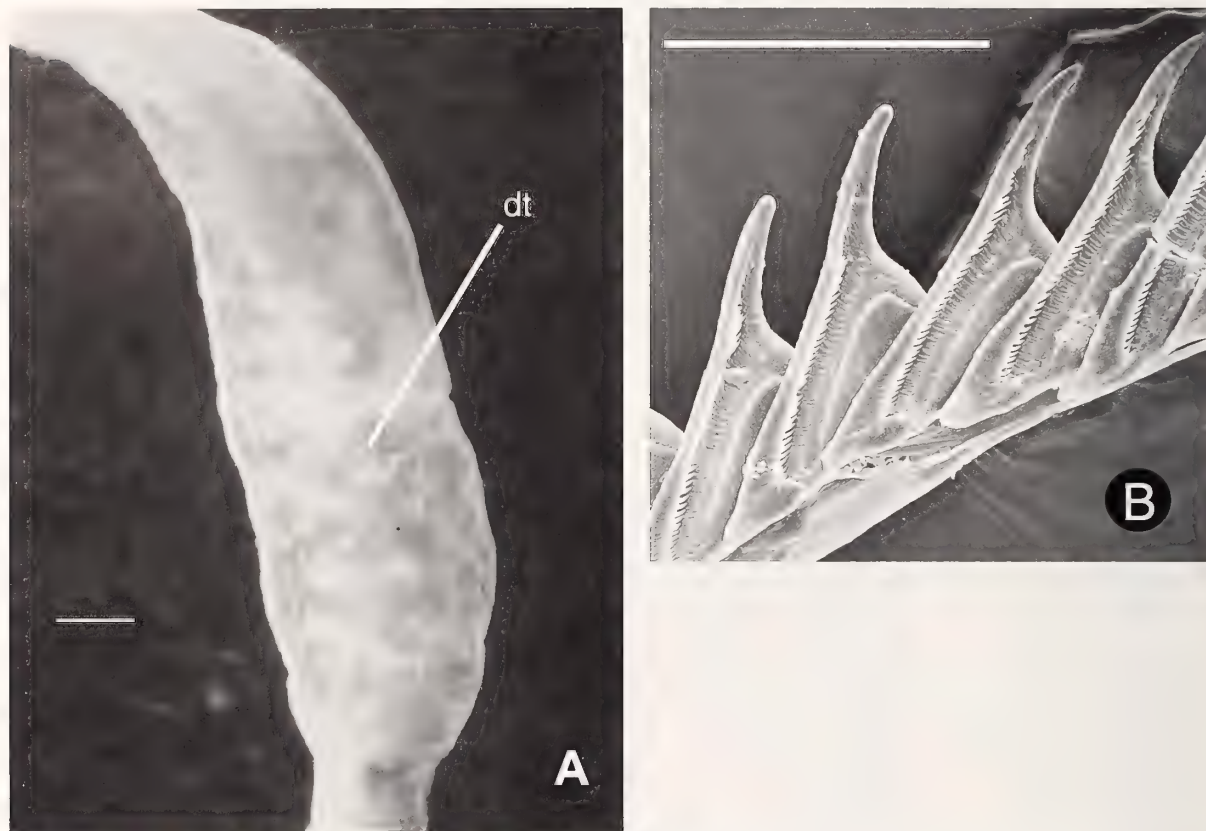


Figure 7. *Phyllodesmium colemani*. **A.** View of digestive tract inside a ceras. **B.** Lateral view of radula. Abbreviations: dt, digestive tract. Scale bars: **A** = 5 mm; **B** = 0.02 mm.

Ryukyu Islands, Japan, 1.5 m depth, 3 April 1993, R.F. Bolland. Two specimens, one dissected, CASIZ 103793, Cathedral Rock, Balayan Bay, Batangas Province, Luzon Island, Philippines, no depth, 25 February 1995, D.W. Behrens.

Distribution: Known from its type locality Okinawa, Japan (Baba, 1991b) and the Philippines (present study).

External morphology (Fig. 1B): Body 56 mm in length, large in size, narrowing uniformly from anterior to posterior end, wide foot, smooth and moderately long rhinophores, oral tentacles shorter in size than rhinophores. Cerata flattened, smooth, with a straight apex, extending outwardly covering the whole dorsum. Ceratal arrangement of one precardiac arch and single vertical rows on each side of the body, lying on distinctive ridges, up to 7 to 8 cerata on each precardiac arch on each side of the body, 8 to 11 cerata on each of the 7 to 9 postcardiac single arches on each side dorsum. Reproductive opening found in right side of dorsum, right below and inside precardiac arch. Renal opening is in interhepatic space, right above the most basal posterior edge of the first postcardiac arch. Anal

papilla on distinctive mound, between first and second postcardiac arches on right side of body.

Cerata and digestive gland branching (Fig. 8C): Cerata flattened, smooth, terminating in a curled apex. Digestive gland branching into secondary and tertiary branches; numerous multiple branches that extend in "web-like" manner, terminating in close proximity to the body wall. Ducts terminate in small chambers, capable of harboring zooxanthellae. Dark brownish-green color present likely due to presence of zooxanthellae in the cerata (Baba, 1991b).

Buccal armature (Figs. 8A–B): Radular formula $63 \times 0.1.0$ (CASIZ 89035). Base of tooth short and wide, long cusp. Denticles visible along center of tooth, separated, short, with blunt tip; masticatory border of the jaw plates has large denticles.

Reproductive system (Fig. 8D): Preampulla duct narrow, long; expanding into large, bulbous, folded ampulla. Ampulla divides into receptaculum seminis and penial complex by thin duct. Penial complex large, connecting to massive and folded albumen gland, opening to a folded, long prostate. Prostate connecting

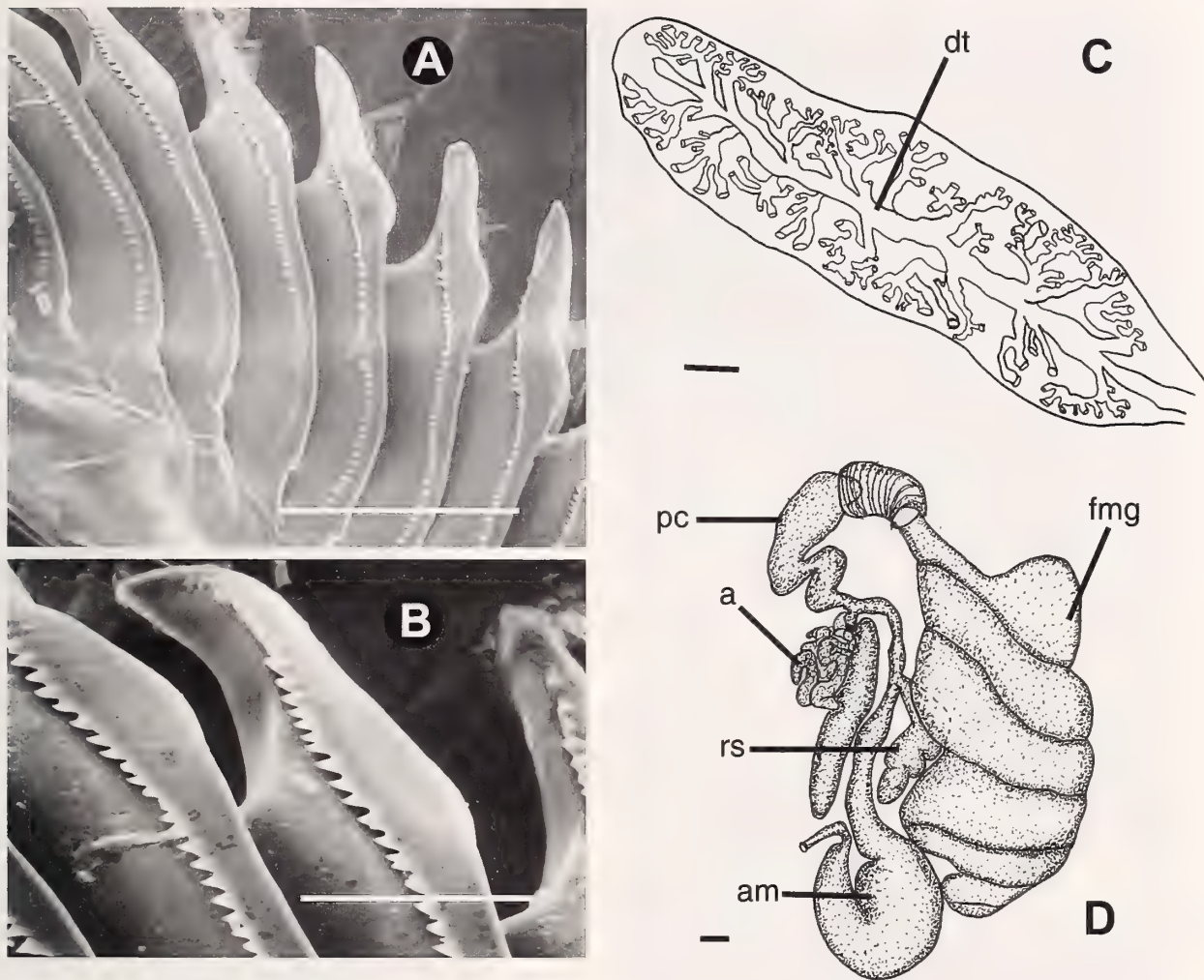


Figure 8. *Phyllodesmium kabiranum*. **A.** Lateral view of radula. **B.** View of radular denticles. **C.** View of digestive tract inside a ceras. **D.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.12 mm; **B** = 0.05 mm; **C** = 12 mm; **D** = 5 mm.

to massive, folded, rectangular shaped female gland mass. Female duct opening into a vagina at base of first cereal cluster on right side of dorsum.

Remarks: Baba (1991) considered *Eolida bella* Rüppel & Leuckart, 1831 as a possible senior synonym of *Phyllodesmium*. Baba noted the similarity in color pattern between the two taxa. However, the remainder of the anatomy of *E. bella* remains unknown. Examination of material from the Red Sea is necessary to confirm the identity of *E. bella*, in order resolve this nomenclatural issue.

***Phyllodesmium macphersonae* (Burn, 1962)**

(Figs. 1D, 9A–D)

Cratena macphersonae Burn, 1962: 118–119, figs. 19–20.

Phyllodesmium macphersonae — Rudman, 1981b: 239–242, 244–261, figs. 12A, B, 17, 21C, 27.

Material examined: One specimen, dissected, CASIZ 115724, Horseshoe Cliffs, Okinawa, Ryukyu Islands, Japan, 3.0 m depth, 29 May 1998, R.F. Bolland. One specimen, CASIZ 104700, 14 km W of Ikei-shima, Tengan Pier, Okinawa, Ryukyu Islands, Japan, 2.1 m depth, 26 August 1994, R.F. Bolland.

Distribution: Originally described from Victoria, Australia (Burn, 1962). Recorded from the Coral Sea (Lord Howe Island) and Tasmania, Australia (Rudman, 1991). Also collected from Japan (present study).

External morphology (Fig. 1D): Body 23 mm in length, of moderate size, extending narrowly from the anterior to the posterior end. Anterior end of foot angular,

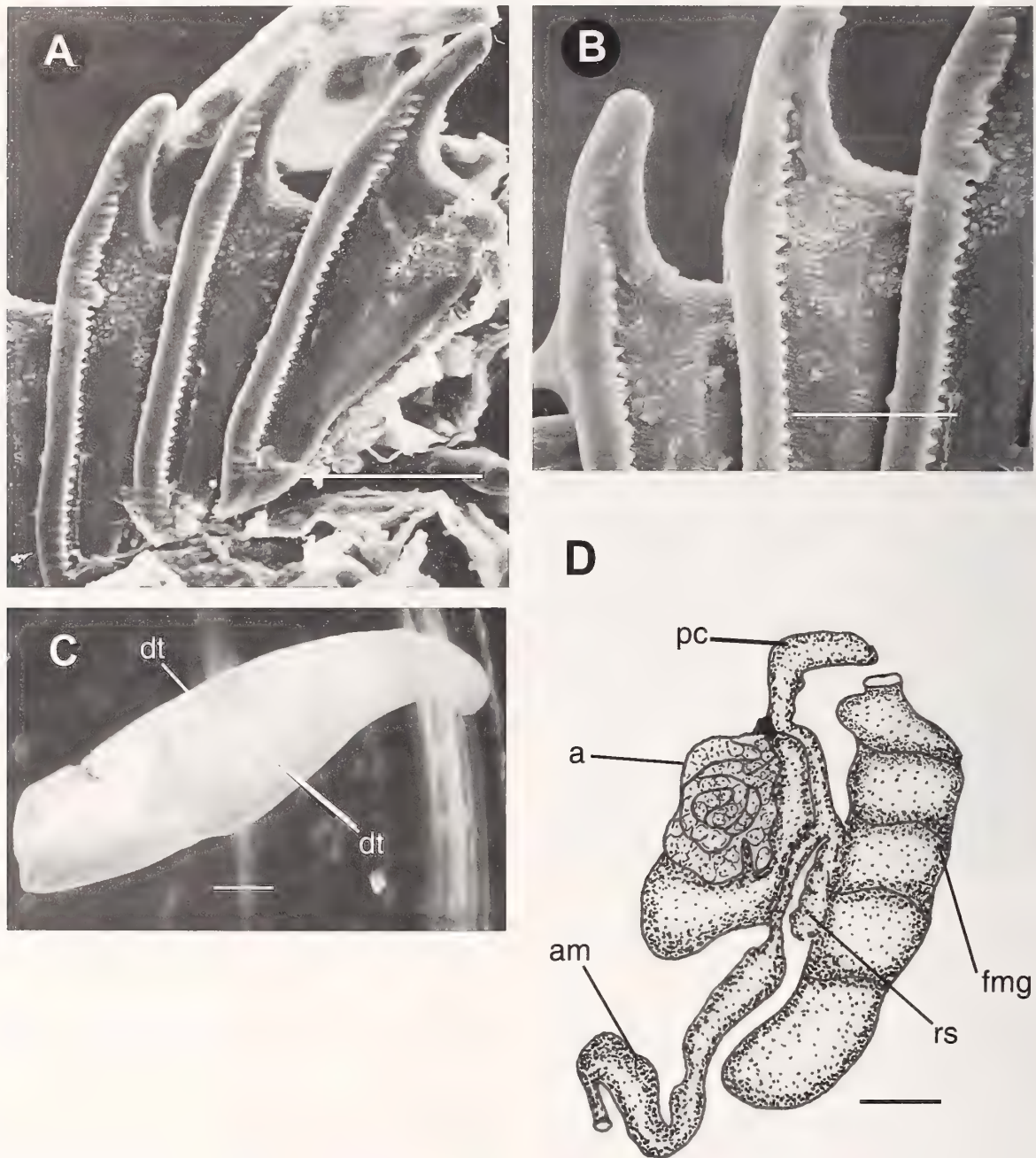


Figure 9. *Phyllodesmium macphersonae*. **A.** Lateral view of radula. **B.** Close up view of radular denticles. **C.** View of digestive tract inside a ceras. **D.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 0.04 mm; **B** = 0.02 mm; **C** = 10 mm; **D** = 5 mm.

narrow, elongate, tapering from the anterior to posterior end. Rhinophores moderately long, smooth, close in size to oral tentacles. Ceratal arrangement of one precardiac arch, up to 6 to 8 single vertical postcardiac rows, up to 6 to 8 cerata on each postcardiac rows on each side of body. Reproductive opening on right side, below anterior basal edge of

precardiac arch. Renal opening immediately above first postcardiac row, in interhepatic space. Anal papilla between first and second postcardiac row, immediately below uppermost postcardiac row.

Cerata and digestive gland (Fig. 9C): Cerata cylindrical, smooth, terminating in curled apex. Digestive

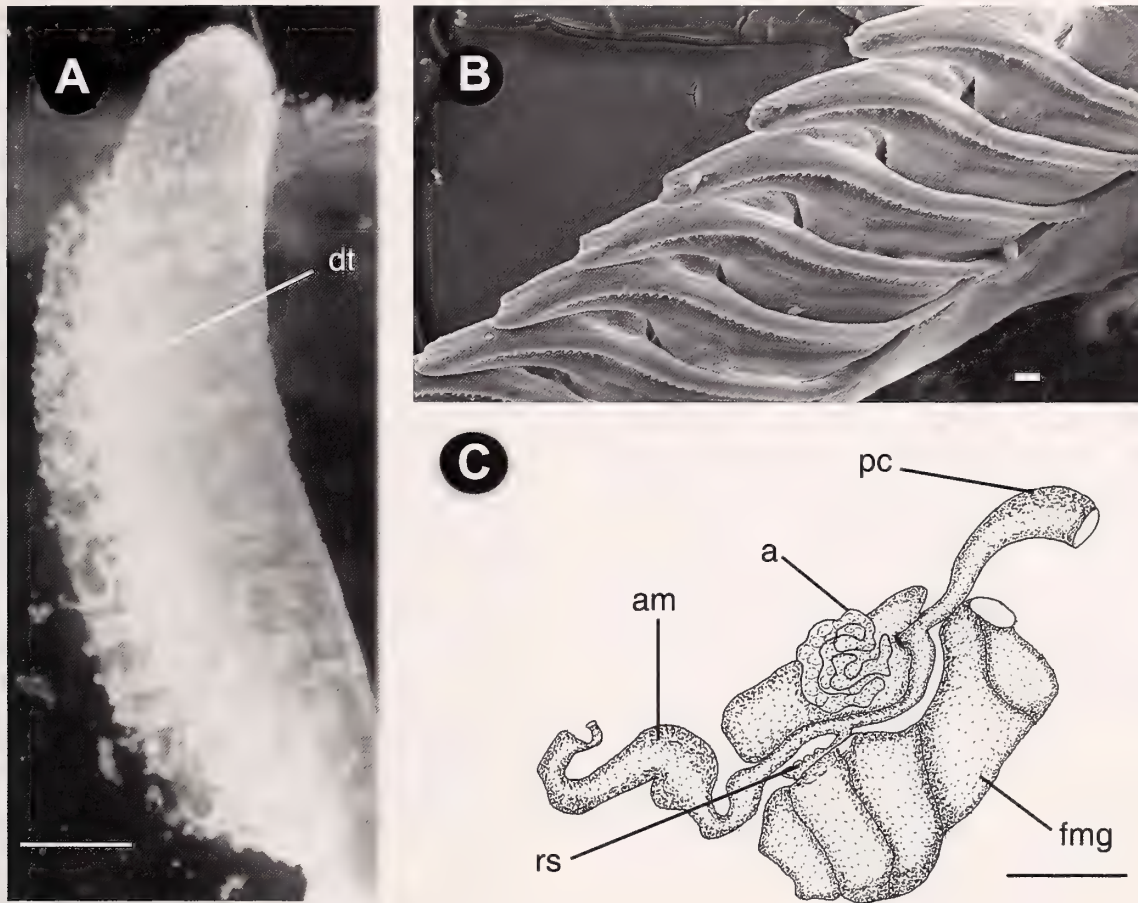


Figure 10. *Phyllodesmium briareum*. **A.** View of digestive tract inside a ceras. **B.** Lateral view of radula. **C.** Reproductive system. Abbreviations: a, albumen gland; am, ampulla; rs, receptaculum seminis; pc, penial complex; fmg, female mass gland; dt, digestive tract. Scale bars: **A** = 10 mm; **B** = 0.01 mm; **C** = 5 mm.

gland composed of central duct running along entire ceras. Photographs of the cerata do not obviously show the detailed structure. However, under close examination through the dissecting microscope, the arrangement of the secondary and tertiary branches was similar to that of *P. magnum*.

Buccal armature (Fig. 9A–B): Radular formula $28 \times 0.1.0$ (CASIZ 65346). Tooth long and narrow base, long cusp. Denticles visible, all along central region of radular teeth, separated, short, terminating in a blunt tip. Masticatory border of jaw smooth (Baba, 1991).

Reproductive system (Fig. 9D): Preampulla narrow, reduced, duct expanding into long and thin ampulla by irregular narrow duct; duct bifurcating into receptaculum seminis and penial complex. Penial complex extending into small and bulbous prostate, which connects to a long, folding and thin female gland mass; female duct opened to a vagina at the base of first ceratal cluster.

Phyllodesmium briareum (Bergh, 1896)

(Figs. 1G, 10A–C)

Ennoia briareus Bergh, 1896: 392–4, Pl. 16, figs. 14, 15.

Phyllodesmium briareus — Gosliner *et al.*, 1996: 177, fig. 627.

Phyllodesmium briareum — Rudman, 1991: 181–187, figs. 13, 14A,B, 15, 16, 17, 27–29.

Material examined: Twenty specimens, CASIZ 065346, Barracuda Point, W side “Pig Island,” near Madang, north coast, Papua New Guinea, 15.2 m depth, 13 January 1988, T.M. Gosliner. One specimen, one dissected, CASIZ 065299, Madang (near lighthouse), north coast, Papua New Guinea, 7.6 m depth, 22 January 1988, T.M. Gosliner. Four specimens, one dissected, CASIZ 83678, Devil’s Point (SW side of Maricaban Island), Maricaban Island, Batangas Province, Luzon, Philippines, 19 February 1992, T.M. Gosliner.

Distribution: Found in the Philippines, Malaysia and Papua New Guinea (Rudman, 1991). Recent studies found *P. briareum* in Japan and Indonesia (present study).

External morphology (Fig. 1G): Body 16 mm in length, moderate size, narrow, reduced (in some cases more elongate). Foot narrow, angular anterior end of corners. Oral tentacles slightly longer than greatly extended rhinophores. Smooth, cylindrical cerata terminating in blunt tip. Ceratal arrangement of one single-rowed precardiac arch, consisting 6 to 8 ceras on each side of body. Reproductive system, renal opening and anal papilla located on right side of body, underneath the precardiac row. Renal opening in the interhepatic space. Anal papilla below first post-cardiac row. Postcardiac cerata in single rows across dorsum on each side of body, each side with 6 to 8 postcardiac clusters with up to 7 ceras on each of them.

Cerata and digestive gland (Fig. 10A): Cerata long, slender, smooth, cylindrical, with branched digestive tract. Digestive tract branching into simple branches, in turn extending into secondary and tertiary branches, making for a dense layer and expansion of the digestive tract all across cerata.

Buccal armature (Fig. 10B): Radular formula $34 \times 0.1.0$ (CASIZ 83678). Base of tooth wide, long, with long cusp. Denticles visible, along central edge of each tooth, short, well-separated, terminating in pointed radular tip. Masticatory border of jaw smooth (Rudman, 1991).

Reproductive system (Fig. 10C): Preampullary duct short, narrow, expanding into bulbous, long and folded ampulla. Ampulla connecting through broad duct to receptaculum seminis and penial complex. Penial complex opening to wide and short prostate through broad duct. Duct connecting to folded albumen gland, located on massive membrane gland. Prostate connecting into folded and long female gland mass.

Phyllodesmium longicirrum (Bergh, 1905)

Myrrhine longicirra Bergh, 1905: 227–9, Pl. 20, figs. 20–29.

Phyllodesmium longicirra — Rudman, 1981b: 242–261, figs. 16, 18–20, 24–27.

Phyllodesmium longicirrum — Rudman, 1991: 195, figs. 26, 28, 29.

Distribution: Described originally from Indonesia (Bergh, 1905), also recorded from the Great Barrier Reef (Rudman, 1991).

Discussion: The anatomy of this species has been described by Rudman (1981b; 1991).

Phyllodesmium pecten Rudman, 1981

Phyllodesmium pecten Rudman, 1981b: 237–239, figs. 14A, 15, 16C, D, E, 27.

Distribution: Known only from its type locality Dar es Salaam, Tanzania (Rudman, 1981b).

Discussion: Anatomy of species described by Rudman, 1981b.

Phyllodesmium opalescens Rudman, 1991

Phyllodesmium opalescens Rudman, 1991: 177–181, figs. 9, 10, 11, 12, 28, 29.

Distribution: Known only from its type locality Hong Kong (Rudman, 1991).

Discussion: Anatomy of species described by Rudman, 1991.

Phyllodesmium horridum (Macnae, 1954)

Favorinus horridus Macnae, 1954: 19–21, figs. 11–13, Pl. 1, fig. 4.

Phyllodesmiopsis horridus — Risso-Dominguez, 1964: 222–238.

Phyllodesmium horridus — Rudman, 1981b: 224.

Phyllodesmium horridum — Gosliner, 1987: 124, fig. 225.

Distribution: Known and described originally from South Africa (Macnae, 1954).

Discussion: Anatomy of species described by Rudman (1981b; 1991).

Phyllodesmium iriomotense Baba, 1991

Phyllodesmium iriomotense Baba, 1991b: 115, figs. 6–7, Pl. 1, fig. 3.

Distribution: Known only from its type locality Okinawa, Japan (Baba, 1991b).

Discussion: Anatomy of species described by Baba, 1991b.

Phyllodesmium guamensis Avila et al., 1998

Phyllodesmium guamensis Avila et al., 1998: 148, figs. 1–10.

Distribution: Only found in its type locality Guam (Micronesia) (Avila et al., 1998).

Discussion: Anatomy of species described by Avila et al., 1998

***Phyllodesmium jakobsenae* Burghardt & Wägele, 2004**

Phyllodesmium jakobsenae Burghardt & Wägele, 2004: 1, figs. 1–5.

Distribution: Known only from Indonesia (Burghardt & Wägele, 2004).

Discussion: The anatomy of this species was completely described by Burghardt & Wägele (2004).

***Phyllodesmium rudmani* Burghardt & Gosliner, 2006**

Phyllodesmium jakobsenae Burghardt & Gosliner, 2006: 31, figs. 1–5.

Distribution: Known only from Indonesia (Burghardt & Gosliner, 2006).

Discussion: The anatomy of this species was completely described by Burghardt & Gosliner (2006).

***Godiva quadricolor* (Barnard, 1927)**

Hervia quadricolor Barnard, 1927: 203, Pl. 20, figs. 9, 10.

Godiva quadricolor — Macnae, 1954: 23–25, text figs. 14–16.

Distribution: This species has been collected from South Africa (Barnard, 1927) and Western Australia (Willan, 1987).

Discussion: Anatomy of species described by Willan (1987). *Godiva* Macnae has been placed on the Official List of Generic Names in Zoology with the name number 1717 (I.C.Z.N., 1966, Opinion 778). The name *quadricolor* Barnard, as published in the binomen *Hervia quadricolor* (type species of *Godiva* Macnae), has been placed in the Official List of Specific Names in Zoology with name number 2148 (I.C.Z.N., 1966, Opinion 778).

***Favorinus japonicus* Baba, 1949**

Favorinus japonicus Baba, 1949: 177, Pl. 43, fig. 151, figs. 135–136.

Distribution: Have been found in Dar es Salaam, Tanzania (Rudman, 1980) and Japan (Baba, 1949) and throughout the Indo-Pacific, extending from the Western Indian Ocean to the Hawaiian Islands (Gosliner, 1980).

Discussion: Anatomy of species described by Baba (1949) and Rudman (1980).

RESULTS

We performed several analyses of the data matrix (Table 3). After several iterations we re-examined the characters. Three characters (14, 21 and 30) were then deleted (using PAUP 4.0 and manually) from the analysis because they are continuous and it is difficult to assess discrete character states. This analysis yielded two trees of 64 steps and consistency and retention indices of 0.469 and 0.730 respectively (Fig. 11). From this analysis, the monophyly of *Phyllodesmium* is supported. Our strict consensus tree shows *Phyllodesmium* as a monophyletic group, supported by a Bremer value of 2 and defined by four synapomorphies: character 12, angular foot corners; character 15, rhinophores smooth or slightly nodular; character 16, masticatory border with a single row of denticles; character 27, cnidosac absent (Fig. 12). Most nodes have a Bremer support value of 1. The third node above the basal node has a value of 3. Additionally, the clade that contains *P. poindimiei*, *P. briareum*, *P. macphersonae* and *P. colemani*, the clade that contains *P. magnum*, *P. longicirrum*, *P. guamensis*, *P. parangatum*, *P. jakobsenae* and *P. rudmani* and the clade containing *P. hyalinum* and *P. crypticum* each have a value of 2.

Our phylogenetic analysis shows that species possessing an unbranched digestive tract (*P. horridum*, and *P. opalescens*) are most basal, while others that have a branched digestive tract are more derived. *Phyllodesmium* species having a branched digestive tract are included in one clade, indicating that elaboration of the digestive gland duct represents a single evolutionary event. Members of this clade share other common traits relating to jaw morphology, ceratal structure, and their ability to store zooxanthellae. Within this group, there is one well-supported clade that divides into two sister clades. The first one is supported by one synapomorphy (narrow foot), while the second is supported by two synapomorphies (ceratal apex curled and tightly congested radular denticles).

Based on the present phylogenetic analysis, some characters used in this study exhibit at least one instance of reversal (indicated by an underline of the character number in Figure 12). Even though the instances of homoplasy are moderate, the phylogenetic reconstruction of the ancestral state is unambiguous. Figure 12 shows some of the characters displaying homoplasy, such as the presence of character 2 in several taxa within different lineages. Several derived characters support distinct phylogenetic relationships within various subclades of *Phyllodesmium*. These derived characters include the presence of zooxanthellae, ceratal morphology (apex, surface, shape) and ceratal arrangement, digestive tract branching, and masticatory border of jaw. Tracing of character trace

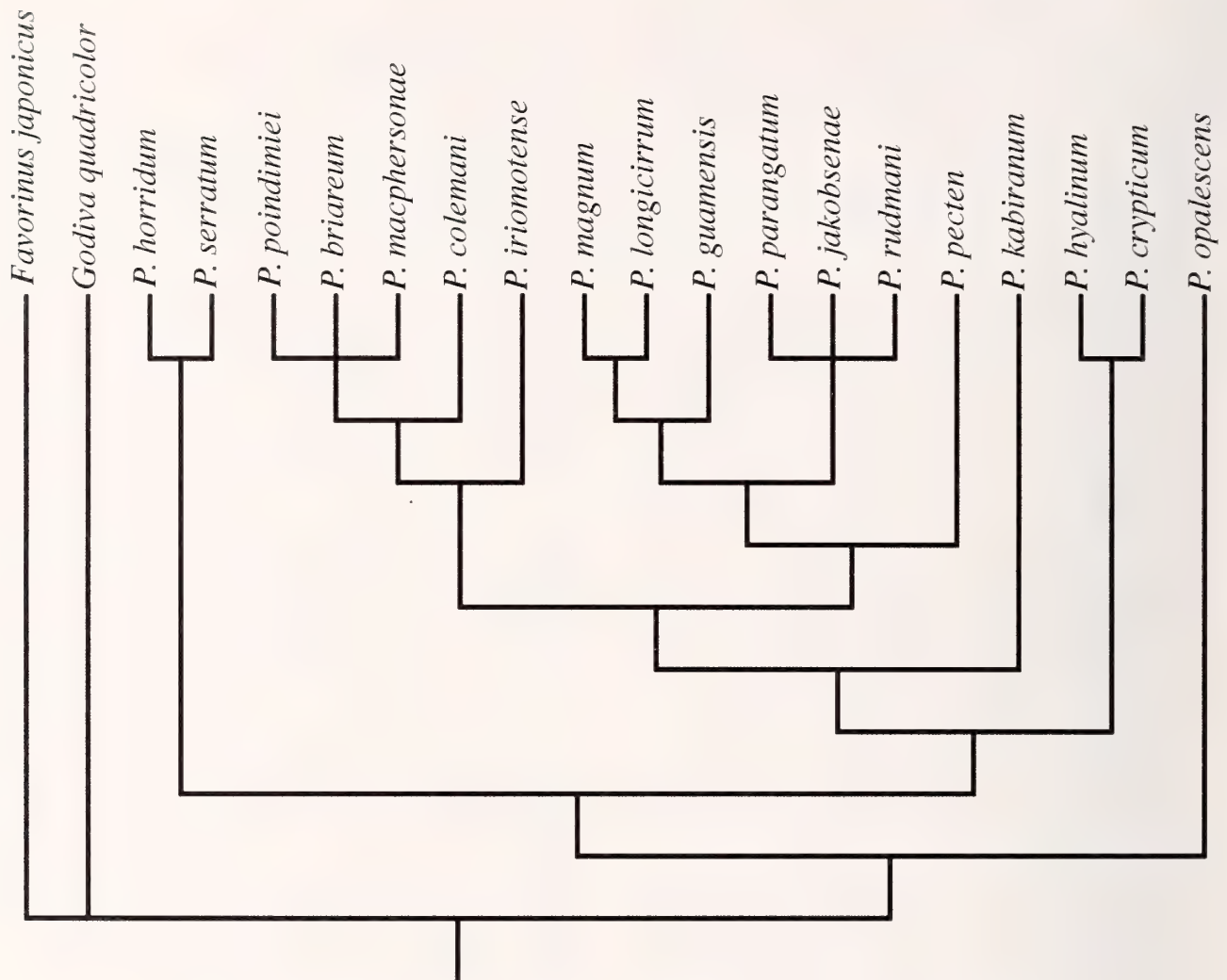


Figure 11. Strict consensus phylogeny of *Phyllodesmium*, (characters 14, 21, 30 excluded).

evolution was made on the not fully resolved consensus tree rather than on one of the two fully resolved trees produced by the phylogenetic analysis. This approach emphasizes the distribution of characters that are consistent rather than those that vary.

DISCUSSION

The phylogenetic analysis carried out in this paper supports the monophyly of the exclusively tropical Indo-Pacific species that have been included in *Phyllodesmium*. In general, the non-parsimony based scenario of evolution suggested by Rudman (1991) is generally upheld by the present phylogenetic analysis. More specifically, our parsimony-based phylogeny supports Rudman's view that more basal members have relatively simple digestive gland branching and more derived taxa have more complex branching of

digestive gland ducts to provide greater surface area for photosynthesis in species that harbor zooxanthellae. However, the arrangement of taxa within Rudman's branching diagram differs in some respects from our phylogeny. For example, Rudman suggested that *P. serratum* was most basal within *Phyllodesmium*, while our analysis suggests that *P. opalescens* is more basal. Additionally, Rudman suggested a continuum of evolution from *P. crypticum* to *P. hyalinum* to *P. pecten*, whereas our analysis suggests that *P. crypticum* and *P. hyalinum* are sister species, while *P. pecten* is a member of another subclade.

Rudman treated evolution within *Phyllodesmium* based on the comparative examination of the digestive system and cerata. However, it is hard to assess how related these assumptions are due to insufficient data regarding the specificity of the feeding specialization across all *Phyllodesmium* taxa. It is evident, though,

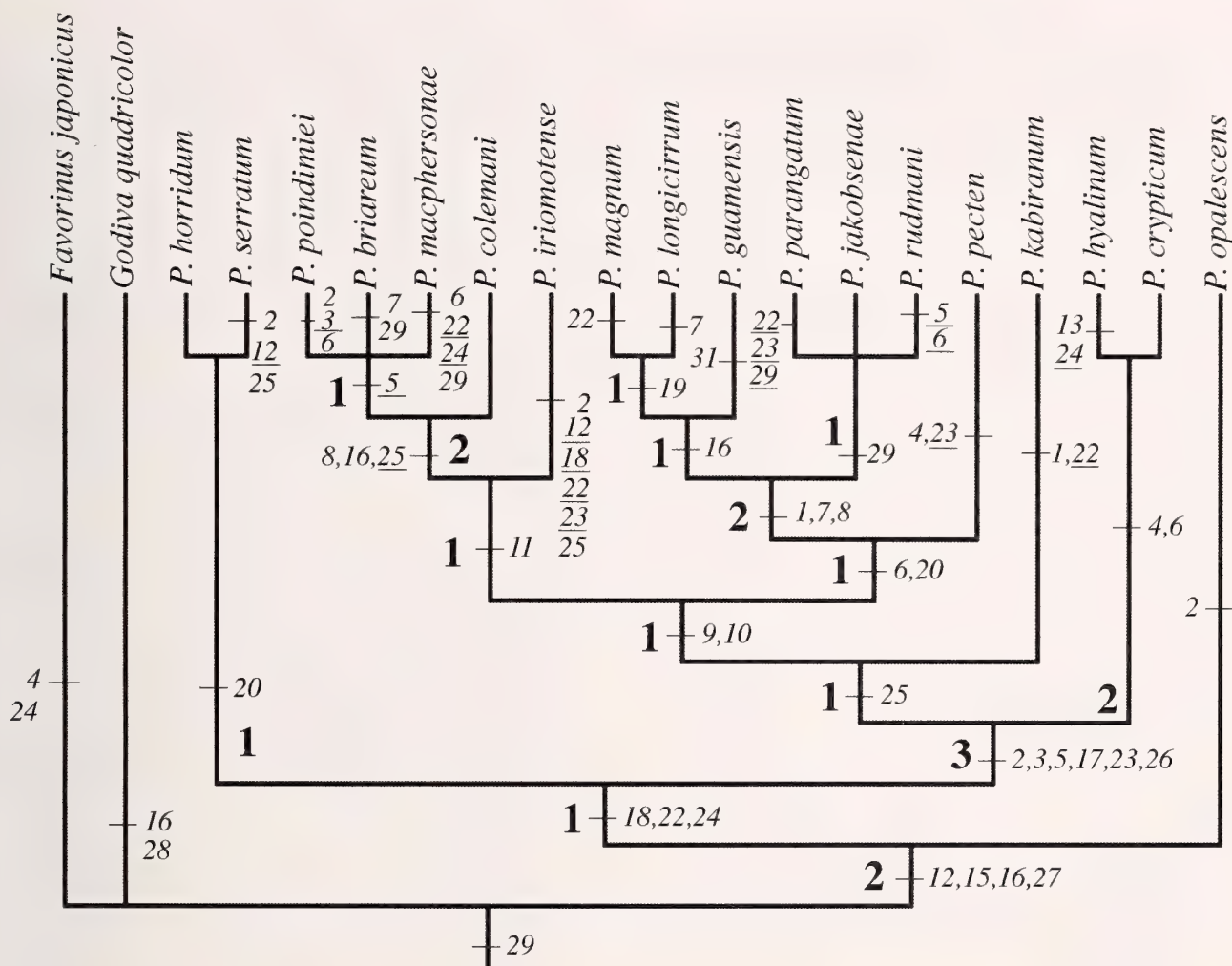


Figure 12. Character and Bremer support analysis of strict consensus tree. Italicized numbers refer to characters contained in text. Underlined numbers indicate instances of reversals. Bold numbers are Bremer support values.

that the morphological changes occurring within *Phyllodesmium* are correlated with their feeding behavior. The increase in size, and the flattening and branching of the digestive tract are all characteristics of the cerata that have developed across taxa of *Phyllodesmium*. These characteristics allow a more efficient means of transporting and accommodating the zooxanthellae, and displaying mimicry of the octocoral coelenterates they prey upon (Rudman, 1981b, 1991).

Histological and digestive dissections on specimens living or freshly preserved material will be needed to assess the ecological interaction occurring across the *Phyllodesmium* taxa. Specimens, used in this study, were fixed in formalin or Bouin's solution making any presence of calcium carbonate octocoral sclerites undetectable and unidentifiable by the observer. Hence, fresh material is needed in order to assess the feeding

sources and ecological interactions occurring between the nudibranch species and its octocoral prey. Further descriptions of *Phyllodesmium* species will help to resolve the phylogenetic relationships and symbiotic relationships within *Phyllodesmium*. In addition, molecular data would aid in providing more information on the evolutionary trend of this genus. Combining these methods would provide a clearer view on the evolution of *Phyllodesmium* and its relationship with its symbionts.

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Earliest Record of the Genus *Haliotis* (Mollusca: Gastropoda) from the Late Cretaceous (Campanian) of Los Angeles County, California

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Abstract. Cretaceous abalone are extremely rare and are known from only two valid species: *Haliotis lomaensis* Anderson, 1902, from the Late Cretaceous (latest Campanian/earliest Maastrichtian) of San Diego County, California and *H. antillesensis* Sohl, 1992, from the Late Cretaceous (late Maastrichtian) of southwestern Puerto Rico. The earliest record of the genus *Haliotis* is here documented from Late Cretaceous (middle middle to late middle Campanian) strata of the Tuna Canyon Formation, Garapito Creek area of Topanga Canyon, Santa Monica Mountains, Los Angeles County, California. This additional Cretaceous record for *Haliotis* could possibly indicate a North American origin for the family Haliotidae.

INTRODUCTION

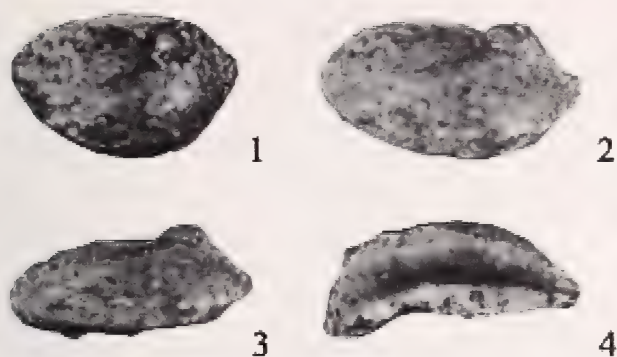
Cretaceous abalone species are extremely rare, currently comprising only two valid species (Sohl, 1992; Geiger & Groves, 1999; Geiger, 2000). These species include: *Haliotis lomaensis* Anderson, 1902 from the Late Cretaceous (latest Campanian/earliest Maastrichtian) Point Loma Formation, San Diego County, California and *H. antillesensis* Sohl, 1992 from the Late Cretaceous (late Maastrichtian) El Rayo Formation, Sabana Grande quadrangle, southwest Puerto Rico. Suspect records of Cretaceous abalone that have been relegated to pleurotomarioidean genera include *Haleotis*? [sic] *antiqua* Binkhorst, 1861 [= *Trochus limburgensis* Kaunhowen, 1897] from the Maastrichtian near Maastricht, Limburg Province, the Netherlands, *Pleurotomaria antiqua* (Binkhorst, 1861) of Weinzettl (1910) from the Late Cretaceous (Cenomanian) near Korycany, Czech Republic, and *Haliotis cretacea* Lundgren, 1894 [= *Pleurotomaria* sp.?] from the Late Cretaceous (Campanian) near Barnakällegrottan, southeastern Sweden [see Sohl (1992) for additional details]. A poorly preserved specimen identified as *Haliotis* sp. by Dawson (1978) and reported by Sundberg (1979, 1984) from the Late Cretaceous (Maastrichtian) Cabrillo Formation of San Diego County, California is actually a specimen of the calyptraeid genus *Lysis* (L.R. Saul, personal communication).

MATERIAL

A single poorly preserved internal mold with little remaining original or recrystallized shell material, Natural History Museum of Los Angeles County, Invertebrate Paleontology (LACMIP) hypotype 13237 (Figs. 1–4) from LACMIP loc. 27110 (ex University of California, Los Angeles loc. 7110) that measures 5.9 mm in overall length retains several diagnostic features that validate it as a haliotid. Observed features include a flattened “shell” with low spire, wide columella, and a row of six tremata toward the left periphery. Because of such poor preservation we hesitate to describe a new species based on this sole example. Nevertheless, due to the uniqueness of this specimen from Late Cretaceous (middle middle to late middle Campanian) strata, it is noteworthy enough to mention as the earliest known worldwide representative of the genus *Haliotis*.

LOCALITY

LACMIP loc. 27110 is on the north side of Garapito Creek just above the 1300 ft. contour line, 900 ft. north, 735 ft. east of SW corner of section 33 (projected), T1N, R16W San Vicente y Santa Monica Land Grant, northeast of Sylvia Park, United States Geological Survey (USGS) Topanga quadrangle (1976 ed.), Santa Monica Mountains, Los Angeles County, California.



Figures 1–4. *Haliotis* sp., hypotype LACMIP 13237, from LACMIP loc. 27110, 1 = dorsal view ($\times 7.6$), 2 = oblique view ($\times 10$), 3 = lateral view ($\times 9.3$), 4 = columellar view ($\times 10.3$).

STRATIGRAPHY & AGE

The specimen was collected by the junior author on 21 December, 1983 from the base of informal “member D” of Wilson (1941) [= map unit Ktd of Yerkes et al. (1994)] within the Late Cretaceous (late middle to early late Campanian), *Metaplocenticeras pacificum* ammonite zone [33N chron] (Elder & Saul, 1996) part of the Tuna Canyon Formation of Yerkes & Campbell (1979) [= Unnamed strata of Dibblee, 1992]. This ammonite zone was cited as Late Cretaceous (middle middle to late middle Campanian) [C33 chron] by Squires & Saul (2003) and we follow this usage. “Member D” is a fossiliferous fine-grained sandstone that occurs immediately above a thick, cobble conglomerate informally designated as “member C” by Wilson (1941) [= map unit Ktc of Yerkes et al. (1994)] and is equivalent to the lowermost part of a fine-grained sandstone reported by Popenoe (1954). LACMIP loc. 27110 is within an unusual small lens of “member D” that disappears along strike within 100 ft. (33 m). Unfortunately, Dibblee (1992) incorrectly mapped this lens of “member D” as Paleocene Santa Susana Formation as did Yerkes et al. (1994). However, recent field work by the junior author combined with the fauna listed below, correctly place the locality within the Tuna Canyon Formation.

In addition to the ammonite *Metaplocenticeras pacificum* (Smith, 1900), LACMIP 27110 also yielded the ammonite *Baculites* cf. *B. inornatus* Meek, 1862, the gastropods *Atira* sp., *Turritella chicoensis pescaderoensis* Arnold, 1908, *Gyrodes pacificum* Popenoe & others, 1987, *Volutoderma* n. sp., and *Biplica obliqua* (Gabb, 1864), and the bivalves *Pterotrignia evansana* (Meek, 1858), *Glycymeris veatchii* (Gabb, 1864), mytilid sp., *Ostrea* sp., and *Calva* sp.

PALEOBIOGEOGRAPHY

Geiger & Groves (1999), Geiger (2000), and Geiger & Poppe (2000) discussed three possible haliotid radiation

models as follows: 1) An “Indo-Pacific” model, also discussed by Lindberg (1992), indicates that living abalone are most diverse in the central Indo-Pacific, which implied that this was their center of radiation; 2) A “Pacific Rim” model proposed by Talmadge (1963), where abalones originated on an island arc from Japan to northern Australia and radiated to California, southern Australia, and the Indo-Pacific; and 3) A “chromosomal” model where species with a low diploid number (28) live in the eastern Mediterranean Sea and species with higher diploid numbers (32) in the Indo-Pacific and (36) in the North Pacific, abalones dispersed eastward from the Mediterranean. However, because these models do not consider the fossil record they could be rejected. Moreover, this confirmation of the earliest known haliotid from Late Cretaceous (middle middle to late middle Campanian) strata of southern California combined with the fact that Cretaceous abalones are known exclusively from North America further strengthens the possibility of a North American origin for the family Haliotidae. Kiel & Bandel (2000) described *Temnotropis frydai* (Family Temnotropidae) from the Late Cretaceous (late Campanian) Valcarga Formation near Torallola, Lérida Province, Catalonia Region, northeastern Spain and speculated that *Temnotropis* is a likely ancestor of *Haliotis*. *Temnotropis* has a *Haliotis*-like shell with a slit rather than a row of tremata. With a possible ancestor in Spain, the haliotids may have originated in the eastern Atlantic (S. Kiel, personal communication, 2007). However, should a haliotid be found in strata older than middle middle to late middle Campanian a reevaluation of their origin will be necessary.

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Predatory Behavior and Diet of *Eupleura sulcidentata* Dall, 1890 (Gastropoda: Muricidae) from West Florida

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Abstract. The diet and feeding behavior of the muricid gastropod *Eupleura sulcidentata* are documented for the first time from laboratory aquarium experiments. *Eupleura sulcidentata* feeds readily on a broad range of shelled invertebrate prey, including barnacles, bivalves and calyptraeid gastropods, by drilling. Drillholes are small (<1 mm) but tend to have beveled sides, a morphology generally regarded as diagnostic of naticid drillholes.

Key Words: Gastropoda, Muricidae, *Eupleura*, predation, diet.

The present study contributes new observations on the diet and feeding behaviors of *Eupleura sulcidentata* Dall, 1890, a diminutive species of ocenebrine muricid with a range that extends from Florida to the Bahamas and northern Cuba. Previously, the feeding biology of this species was studied by Radwin and Wells (1968), who found *E. sulcidentata* difficult to maintain in captivity. In their experiments, *E. sulcidentata* predators were offered several types of invertebrate prey, including the bivalves *Crassostrea virginica*, *Ostrea equestris*, and *Brachidontes exustus*, and two barnacles, but refused all five and eventually died without feeding.

Predatory gastropods of the family Muricidae are well known for their capacity to drill holes in shelled invertebrate prey (Carriker, 1961, 1981; Carriker and Gruber, 1999; Carriker et al., 1974), but many muricids employ additional (or alternative) modes of food acquisition, including use of anesthetizing toxins (West et al., 1994; Roller et al., 1995), mechanical shell breaking and wedging (Wells, 1958; Dunkin and Hughes, 1984; Perry, 1985), ovophagy (Philipps, 1969; Taylor, 1976; Abe, 1983), kleptoparasitism (Ishida, 2001, 2004), carrion feeding (Wu, 1965; Morton, 1994), and true parasitism (Ward, 1965; Robertson, 1970; Matsukuma, 1977). Given this diversity, it is possible that *E. sulcidentata* is an obligate non-driller specializing on prey other than those provided by Radwin and Wells (1968).

As an initial test of this hypothesis, we repeated the Radwin and Wells experiment using prey known to occur in the same microhabitat as *E. sulcidentata*. At least one of the prey species offered in the Radwin and Wells study, the oyster *C. virginica*, lives in muddier, lower salinity waters of the upper estuary, whereas *E. sulcidentata* is found only in sandier, normal marine

conditions of the lower estuary and shallow coast. Thus, in at least one case, *E. sulcidentata* may have simply been refusing an unfamiliar prey.

Although *E. sulcidentata* is not uncommon, its cryptic microhabitat makes it difficult to observe its feeding preferences and behaviors in the field. In Tampa Bay, Florida, *E. sulcidentata* is most common in tidal channels between mangrove islands, where the channels are paved with the disarticulated valves of the venerid clam *Mercenaria campechiensis* (Gmelin, 1791). When oriented in a hydrodynamically-stable, concave-down position, large *Mercenaria* valves create a cave-like domicile for *E. sulcidentata* and numerous other small invertebrates. Because of their local abundance and close proximity to *E. sulcidentata*, these other invertebrates are the most likely components of the diet of *E. sulcidentata*.

Predators and prey in this experiment were collected between December 2005 and February 2006 in 1–2 m of water from Miguel Bay, in the southernmost region of Tampa Bay, Florida and transferred to a laboratory at the University of South Florida in Tampa. Six *E. sulcidentata*, all roughly 20 mm in shell length (maximum shell length of this species) and presumably mature, were collected from the field site, all of them underneath overturned *Mercenaria* valves. Nine shelled invertebrates encountered with *E. sulcidentata* predators in this microhabitat were collected and offered as food in this experiment, including the barnacle *Balanus eburneus* Gould, 1841; five species of bivalve: *Ostrea equestris* Say, *Brachidontes exustus* (Linnaeus, 1758), *Timoclea grus* (Holmes, 1858), *Lyonsia floridana* Conrad, 1849, and *Anomalocardia auberiana* (d'Orbigny, 1842); two species of slipper limpet: *Bostrychopulus aculeatus* (Gmelin, 1791) and a member of the

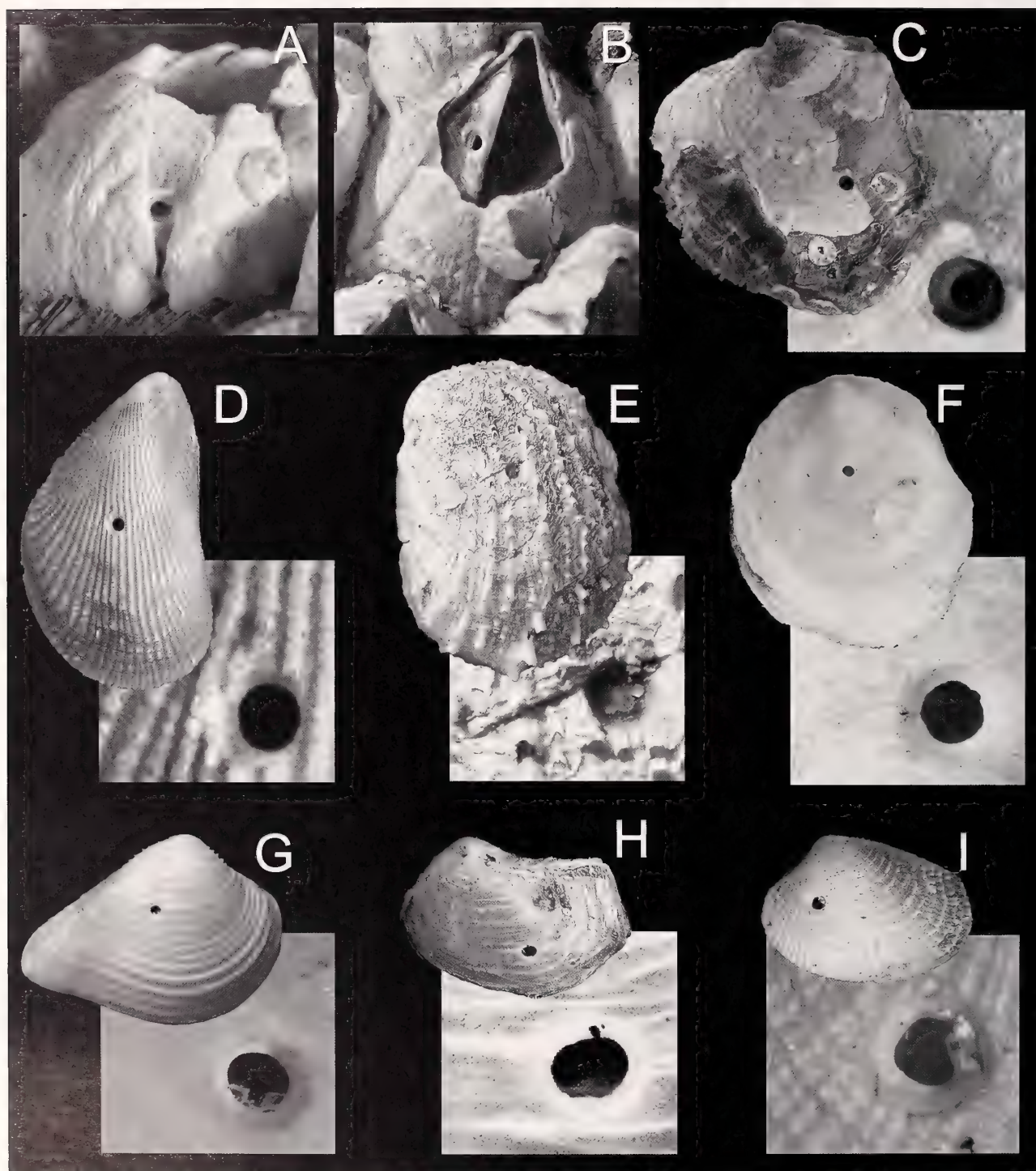


Figure 1. Examples of predatory drillholes produced by the muricid gastropod *Eupleura sulcidentata* in barnacle, bivalve, and gastropod prey. Length measurements are for the anterior-posterior shell axis unless otherwise stated. A. *Balanus eburneus* (height 4.3 mm). B. *Balanus eburneus* (height 5.1 mm). C. *Ostrea equestris* (15.2 mm). D. *Brachidontes exustis* (5.9 mm). E. *Bostrycapulus aculeatus* (14.4 mm). F. *Crepidula depressa* (15.5 mm). G. *Anomalocardia auberiana* (13.2 mm). H. *Lyonsia floridana* (6.9 mm). I. *Timoclea grus* (7.3 mm).

Crepidula plana species complex, probably *Crepidula depressa* Say, 1822 (see Collin 2001), and the chiton *Isnochiton papillosus* (C. B. Adams, 1845).

The six predators were housed in a single 10-gallon laboratory aquarium with recirculating seawater (changed weekly) from the bay. Seawater was maintained at a constant salinity of 35 ppt and a temperature of 15–18°C to mimic conditions at the field site during the time of collection. Within the aquarium, predators were isolated from one another by placing each in its own 10 × 7 × 5 cm clear plastic box into which ten 0.5 cm diameter holes had been drilled. The holes provided ample water circulation, and the box is approximately the same volume as the cryptic microenvironment beneath disarticulated *Mercenaria* valves. The boxes also allowed us to observe the activities of individual predators and monitor the feeding experiments continuously.

Prey were offered one species at a time to predator boxes, except for *Crepidula* and *Bostrycapulus*, which were collected on the same *Mercenaria* valve and offered simultaneously to a single predator. Cemented prey, such as oysters and barnacles, and sessile, loosely attached prey, such as *Brachidontes* and *Crepidula*, which were found attached to the interiors of *Mercenaria* shells, were introduced to the boxes on the original *Mercenaria* shell cut down to 5 cm² pieces.

All dead prey shells were removed prior to introducing the *Mercenaria* piece to the predator. *Anomalocardia*, which is free-living and shallowly infaunal, was added to a box with sand 1 cm deep to allow natural burial and to determine whether the predator could excavate buried prey. Feeding experiments were monitored over a 2-month period, and predated shells were removed daily.

Eupleura sulcidentata fed readily upon eight of the nine prey species offered, the exception being the highly mobile *Isnochiton papillosus*, which was never attacked and experienced no mortality during the experiment. All other prey species were successfully drilled and eaten, in contrast to the results of the Radwin and Wells (1968) experiment. *Eupleura sulcidentata* predators produced drillholes with a mean outer borehole diameter of 0.57 mm ± 0.085 (n = 40) and, in most cases, beveled sides (i.e., a naticid-like morphology). Drillholes in *Anomalocardia* were more often straight-sided (i.e., a more typical muricid-like morphology), but this was still variable depending on local shell thickness at the site of the drillhole. Thus, *E. sulcidentata* joins the growing list of muricid gastropods capable of drilling beveled naticid-like drillholes (see also Edward et. al., 1992; Gordillo and Amuchástegui, 1998; Carriker and Yochelson, 1968).

Predators selected drilling sites away from the prey shell margins for attacks on bivalves and slipper limpets. However, 50% of barnacle prey consumed (n

= 8) were edge drilling attacks between wall plates. Only one attack on *B. eburneus* was a drillhole through a wall (lateral plate), and the remainder (n = 3) were drillholes through the beak (scutum). The more refined attack behaviors used against barnacles suggests that *E. sulcidentata* may specialize on this prey type in the wild.

For drilling attacks recorded on the slipper limpets *C. depressa* and *B. aculeatus*, 42% (5/12) resulted in incomplete drillholes and unsuccessful attacks. No obvious defensive responses by the slipper limpets were observed during the course of the experiment, although all were mobile and periodically changed their position on the *Mercenaria* shell or even moved onto the interior of the plastic box. The ratio of incomplete drillholes to total drilling attempts was higher for the spiny *Bostrycapulus* (67%, 2/3) than the smooth surfaced *Crepidula* (33%, 3/9), although these numbers are not statistically significant. It is notable, however, that the predator offered the slipper limpets selectively drilled all of the non-spiny *C. depressa* first. Only when the nine unornamented *C. depressa* had been eliminated from its box did *E. sulcidentata* begin to attack and drill the spiny *Bostrycapulus*.

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A Large New Species of *Lobatus* (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with Notes on the Genus

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Abstract. A very large new stromb is described from the Neogene of the Dominican Republic, *Lobatus vokesae* sp. nov. *Lobatus* is used here as a genus to include the Tropical American clade of species previously placed in the subgenus *Tricornis*. The new species has characters in common with all the various subgenera proposed within the genus, making subgeneric assignment of this early member of the genus *Lobatus* undesirable.

Key Words: Gastropoda, *Lobatus*, new species, systematics, Neogene, Dominican Republic.

INTRODUCTION

The Strombidae are a group of tropical to subtropical gastropods, predominantly inhabiting the intertidal and subtidal zones, feeding on macroalgae and epiphytes (Robertson, 1961; Berg, 1975). Species in this family are conspicuous because of their medium-sized to very large, solid, heavy shells.

The early and late Miocene deposits on the island of Hispaniola, and more specifically the outcrops occurring along the Cibao valley of the Dominican Republic, are well known for their fauna of Strombidae. Sowerby (1850) was the first to describe fossil mollusks from these rich localities and named three species of *Strombus*. Subsequent workers such as Maury (1917) and Pilsbry & Johnson (1917) have brought the number of strombid taxa known from these deposits to nine (Table 1). However, this is far from being a comprehensive list of the strombid taxa occurring in the Dominican Republic. Our own collections (BL) include probably four undescribed species, the most spectacular of which is described in this paper.

SYSTEMATIC DESCRIPTION

Genus *Lobatus* Iredale, 1921

Type species: (by monotypy, Iredale, 1921: 208): - *Strombus bituberculatus* Lamarck, 1822: 690. Junior subjective synonym of *S. raninus* Gmelin, 1791: 3511. Recent, West Indies and Florida.

Remarks: Throughout the Neogene, the Strombidae have formed an important part of tropical American assemblages, especially in the western Atlantic, where they diversified into numerous species and formed several distinct species groups. Classically, Neogene tropical American *Strombus* species have been placed in three genera or subgenera; *Strombus* (s.s.) [type species *S. pugilis* Linnaeus, 1758, by subsequent designation, Recent, western Atlantic], *Lentigo* Jousseaume, 1886 [type species *Strombus lentiginosus* Linnaeus, 1758, by monotypy, Recent, East Africa], and *Tricornis* Jousseaume, 1886 [type species *Strombus tricornis* Lightfoot, 1786, by monotypy, Recent, Indo-Pacific]. The new species described in this paper belongs to the last group.

Table 1

Preliminary list of strombid taxa so far recorded from the Neogene Dominican Republic. Column 1: the original name under which the taxon was described; column 2 the formation in which it occurs (recorded from literature and BL collections); column 3: original references and subsequent references with figures. Sowerby's (1850) type material was illustrated by Pflug (1961).

Taxon	Formation	Reference
<i>Strombus haitensis</i> Sowerby, 1850	Gurabo and Cercado	Sowerby, 1850, p. 48, pl. 9, fig. 7 Pflug, 1961, p. 26–27, pl. 3, figs 1, 2, 3, 5, 6, 8
<i>Strombus proximus</i> Sowerby, 1850	Gurabo and Cercado	Sowerby, 1850, p. 48, pl. 9, fig. 8 Pflug, 1961, p. 24–26, pl. 2, figs 5, 6, 8, 9, 10
<i>Strombus bifrons</i> Sowerby, 1850	Gurabo	Sowerby, 1850, p. 48, pl. 9, fig. 9 Pflug, 1961, p. 27–28, pl. 4, figs 1–4, 7, 8, 10
<i>Strombus ambiguus</i> Sowerby, 1850	Unknown	Sowerby, 1850, p. 48 Pflug, 1961, p. 28–29, pl. 4, figs 5, 6, 9
<i>Strombus pugiloides</i> Guppy, 1866	?Cercado	Maury, 1917, p. 120, pl. 20, fig. 6 Pflug, 1961, p. 23–24, pl. 3, figs 4, 7
<i>Strombus maoensis</i> Maury, 1917	?Mao	Maury, 1917, p. 120, pl. 21, fig. 1
<i>Strombus galliformis</i> Pilsbry, 1917		Pilsbry, 1917, p. 170
<i>Strombus dominator</i> Pilsbry, 1917	Gurabo	Pilsbry & Johnson, 1922, p. 366, pl. 31, figs 1–2 Pilsbry, 1917, p. 170
<i>Strombus (Lentigo) cf. raninus</i> Gmelin, 1791	Gurabo	Pilsbry & Johnson 1922, p. 366, pl. 32, figs 1, 9 Jung & Heintz, 2001, p. 44, fig. 19

The systematics of *Tricornis*, however, require revision. A molecular phylogeny of strombids shows that *Tricornis* is polyphyletic and comprised of separate, distantly related tropical American and Indo-Pacific clades (Latiolais et al., 2006). Kronenberg & Lee (2007) argued that *Lobatus* Iredale, 1921 [type species *Strombus bituberculatus* Lamarck, 1822, by monotypy, Recent Caribbean (junior subjective synonym of *S. raninus* Gmelin, 1791)] is the first available name for the tropical American group previously known as *Tricornis* (sensu Abbott, 1960).

In this paper, we treat *Lobatus* as a full genus, as this clade is separated from all other strombids, including *Strombus* (s.s.), by one of the longest and best-supported branches in the strombid molecular tree. Notably, this conflicts with the tree topology of strombids inferred from anatomical data (Simone, 2005). However, the Latiolais et al. (2006) phylogeny is based on an analysis of nearly three times as many strombid taxa and at least twice the number of phylogenetically informative characters as Simone's (2005) tree, and is less likely to change as more data are added.

Whether and how the *Lobatus* group should be divided into subgenera is not entirely clear with the data at hand. Based on shell features, Petuch (2004) subdivided the tropical American species of *Tricornis* into several subgenera: *Aliger* Thiele, 1929 [type species *Strombus gallus* Linnaeus, 1758, by monotypy, Recent, Caribbean], *Eustrombus* Wenz, 1940 [type species *Strombus gigas* Linnaeus, 1758, by original designation, Recent, Caribbean], *Macrostrombus* Petuch, 2004 [type species *Strom-*

bus costatus Gmelin, 1791, by original designation, Recent, Caribbean] and *Titanostrombus* Petuch, 2004 [type species *Strombus goliath* Schröter, 1805, by original designation, Recent, Brazil]. It should be noted that Petuch (1994) regarded all these as subgenera of *Strombus*, and employed *Lobatus* in the same fashion, viz. a subgenus of *Strombus*. The molecular phylogeny of Latiolais et al. (2006) shows *S. gallus*, *S. gigas* and *S. costatus* to be very closely related.

The genus *Lobatus* Iredale, 1921 was introduced without a description. *Lobatus* is defined here as a clade of medium sized to very large strombs with widely expanding, *non* digitated, outer lips, and a glazed outer edge of the rim of the outer lip, not bent toward the columella when reaching maturity, usually with strong spiral sculpture on the last whorl. This clade is in Recent times restricted to the Caribbean and Panamic faunal Provinces. It is first recorded from the Lower Miocene Chipola Formation of Florida as *Strombus chipolanus* Dall, 1890 (Gardner, 1947; Petuch, 2004) and the Middle Miocene Baitoa Formation of the Dominican Republic by another undescribed species (Bernard Landau unpublished data). *Lobatus* is represented in the Late Miocene to Early Pliocene Dominican Republic assemblages by *S. haitensis*, *S. galliformis*, *S. dominator*, *S. raninus* and *Lobatus vokesae* sp. nov. *Strombus maoensis* Maury, 1917 was based on a single incomplete shell, and despite intensive collecting we have found no further specimens. Maury (1917) compared *S. maoensis* to *S. gallus*, and it probably represents a species of *Lobatus*. *Strombus ambiguus* Sowerby, 1850 is also based on a

juvenile specimen of a *Lobatus* species (lectotype illustrated by Pflug, 1961).

Abbreviations: The following abbreviations are used: NMB = Naturhistorisches Museum Basel localities; TU = Tulane University localities; NHMW = Naturhistorisches Museum in Wien (Austria) collection number; BL coll. = Bernard Landau collection.

SYSTEMATIC DESCRIPTION

Genus *Lobatus* Iredale, 1921

Type species: (by monotypy, Iredale, 1921: 208): - *Strombus bituberculatus* Lamarck, 1822: 690 (junior subjective synonym of *S. raninus* Gmelin, 1791: 3511), Recent, West Indies and Florida.

Lobatus vokesae Landau, Kronenberg and
Herbert sp. nov.

(Figures 1–7)

Etymology: We have great pleasure in naming this magnificent shell in honor of Emily Vokes for her enormous contribution to Caribbean Neogene paleontology.

Description: (Based on holotype and paratype) Shell very large, solid, when complete reaching at least 270 mm high. Protoconch not known. Seven teleoconch whorls preserved. Spire broadly conical, weakly coeloconoid in profile, spire whorls depressed in holotype; fifth and penultimate whorls slightly elevated and roundly shouldered in paratype. Sculpture on early teleoconch whorls of small rounded tubercles placed immediately above abapical suture, crossed by numerous fine spiral threads. Abapically tubercles become weaker, subobsolete on fourth whorl, and spiral threads broaden to form relatively narrow, flattened, subequal spiral cords. Suture impressed, crenulated around tubercles on early teleoconch whorls, weakly undulating abapically. Last whorl greatly inflated, bearing three large, roundly pointed tubercles at shoulder, first tubercle placed opposite (to left of) aperture, third on dorsum, second tubercle midway between other two. Dorsal tubercle very strongly developed, first tubercle slightly smaller, intermediate tubercle weakest. Spiral sculpture of broad, flattened, primary spiral cords, only clearly developed on mid-portion of last whorl, where there are 10–13 cords, and numerous irregular flattened secondary cords. Growth lines prominent on portions of last whorl, interrupting secondary cords, giving a somewhat reticulate aspect to parts of dorsum. Outer lip not thickened, greatly expanded, its apical end extended above height of apex (when outer lip complete) and expanded medially to join ventral midline. Outer edge of lip and strombid

notch not preserved. Parietal wall smooth. Base of columella strongly bent backwards. Siphonal canal open, relatively long and broad, bent slightly to right and weakly posteriorly recurved.

Holotype: NHMW 2007z0161/0001

Dimensions of holotype: Length 220 mm; dorso-ventral height (restored) 165 mm; width 190 mm (Figures 1–3).

Type locality: Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15).

Material: Holotype; and 1 Paratype (B. Landau coll.), length 264 mm; dorso-ventral 150 mm; width (incomplete outer lip) 180 mm (Figures 4–7); locality Cañada de Zamba, off Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15).

Remarks: This species is based on two adult specimens from different localities along the Rio Cana, the holotype from beds of late Miocene age, the paratype from basal Pliocene beds. Neither of the specimens is perfect; both are missing the outer part of the outer lip (more complete in the holotype), and the holotype has the top of the dorsal tubercle abraded. The paratype shows signs of damage during life, possibly as a result of attack by a predator, and subsequent repair, with an irregular fracture line running the whole length of the last whorl.

There are some differences between the two specimens; the paratype when complete would have been the larger shell. It has a slightly more elevated spire than the holotype, and the tubercles at the shoulder of the last whorl are even more massive than in the holotype.

Comparisons: *Lobatus vokesae* sp. nov. is similar in size to the Recent *Lobatus gigas*, and both species have a broadly expanded but not thickened outer lip. The character of their spires, however, is quite different, as it is much more elevated in *L. gigas* than in *L. vokesae* n. sp., with all the spire whorls bearing pointed tubercles and a greater number of more pointed tubercles on the shoulder of the last whorl. The first record of *L. gigas* is from the Bowden Formation of Jamaica (Jung, 1971). The Bowden Formation is usually considered late Miocene to early Pliocene (Berggren, 1993) or early Pliocene (Bolli & Bermudez, 1965; Bolli & Premoli Silva, 1973; Jung & Heitz, 2001), although Aubry (1993) placed them in the early late Pliocene (calcareous nannoplankton zone NN16). It has been suggested to us that the Bowden Formation is an olistostrome, which would account for these different ages (Oliver Macsotay, personal communication,



Figures 1–3. *Lobatus vokesae* Landau, Kronenberg and Herbert sp. nov. Holotype, NHMW 2007z0161/0001. Locality: Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15). Length 220 mm; dorso-ventral height (restored) 165 mm; width 190 mm.

2007). *Lobatus gigas* has not been found in the Dominican Republic assemblages.

The Recent *Lobatus goliath* Schröter, 1805 has an even larger shell, also with a non-thickened outer lip, which is even more widely expanded than in the *L. vokesae* sp. nov. or *L. gigas*. The spire of *L. goliath* is similar to that of our new species; depressed, devoid of tubercles (or almost so) and with a coeloconoid profile,

but the tubercles on the last whorl are more numerous and far less strongly developed than in *L. vokesae* sp. nov. We are not aware of any fossil record for *L. goliath*. *Lobatus williamsi* (Olsson & Petit, 1964) from the late Pliocene of Florida, allocated to *Titanostrombus* by Petuch (1994), also lacks the large shoulder tubercles on the last whorl of our new species, but it has some distinct knobs on the shoulder of the



Figures 4–7. *Lobatus vokesae* Landau, Kronenberg and Herbert sp. nov. Paratype, BL coll. Locality: Cañada de Zamba, off Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15). Length 264 mm; dorso-ventral 150 mm; width 180 mm.

penultimate whorl (Petuch, 1994: pl. 20, fig. A) that are not present in *L. vokesae* sp. nov.

The characters of the tubercles and the depressed spire, almost devoid of sculpture, are similar to those of the Recent Florida species *Lobatus costatus* Gmelin, 1791. However, in *L. costatus* the outer lip is not so greatly expanded, especially in the adapical portion, and is very strongly thickened. *L. costatus* is also a smaller species and lacks the complex spiral sculpture of primary and secondary cords present on the last whorl of *L. vokesae*. Petuch (1994) described a subspecies *Strombus (Macrostrombus) costatus griffini* Petuch, 1994 from the Late Pliocene of Florida. The shell illustrated (Petuch, 1994, pl. 19, fig. H) and numerous topotypes in the BL collection all have much weaker tubercles than the Recent shell or *L. vokesae* and we agree that they are not conspecific. However, several other *Strombus (Macrostrombus)* species were described in the same publication, very similar to this subspecies, and a review of these taxa is beyond the scope of this work. *Lobatus costatus* occurs fossil in the Pleistocene Tortuga Formation of Cubagua Island, Venezuela (Bernard Landau unpublished data).

Within the Dominican assemblage, *Lobatus vokesae* sp. nov. is most similar to *L. dominator* in the character of its very prominent dorsal tubercle. However, *L. dominator* has a much smaller shell (less than half the size of *L. vokesae*), the primary spiral cords on the last whorl are more distinct, and the shape of the outer lip is quite different. We (BL coll.) have six specimens of *L. dominator* from the Cercado and Gurabo Formations of the Dominican Republic. These specimens are highly variable, and in the largest the adapical extremity of the outer lip is developed into an open digitation, similar to but not as elongated as that seen in the Recent Caribbean species *L. gallus* (Linnaeus, 1758). *Strombus dominator delabechei* Rutsch, 1931, described from the Bowden Beds of Jamaica, probably falls within the range of variation of Dominican Republic specimens.

The shells of *Lobatus vokesae* sp. nov. demonstrate characters intermediate between those of the subgenera *Eustrombus* (very large, greatly expanded and not thickened outer lip), *Macrostrombus* (ribbed last whorl sculpture, large tubercles at the shoulder) and *Titanostrombus* (very large size, combined with a low, coeloconoid spire) as recognized by Petuch. Therefore, it seems undesirable to assign *L. vokesae*, an early species of *Lobatus*, to any subgenus within the genus *Lobatus*. In the more Recent fossil record fairly well defined lineages can be recognized within *Lobatus*.

The origins of the genus *Lobatus* are unclear at present, but it is likely that it arose from a species which would be allocated to *Persististrombus* Kronenberg & Lee, 2007. Within *Persististrombus* there are some tendencies towards *Lobatus*-like species (Harzhauser & Kronenberg, in prep.).

Geological and environmental setting: The holotype is from the Rio Cana, area equivalent to NMB 16832/16833 and TU 1230, Cercado Formation (late Miocene) (Saunders et al., 1986, text-figure 15). This is a 50 cm thick bed with closely packed small molluscs in which *Astraea* Röding, 1758 and *Tegula* Lesson, 1835 predominate. Other common gastropods are *Erosaria spurca* (Linnaeus, 1758), *Pachycrommium guppyi* (Gabb, 1873), *Polinices subclausa* (Sowerby, 1850), *Neverita (Hypterita) nereidis* (Maury, 1917) *Semicassis reclusum* (Guppy, 1873) and *Chicoreus cornurectus* (Guppy, 1876). These probably represent shallow inshore conditions.

The paratype is from the Cañada de Zamba locality, a tributary of the Rio Cana, area equivalent to NMB 16817 and TU 1354, Gurabo Formation (base of the Pliocene) (Saunders et al., 1986, text-figure 15). This locality has a rich and varied gastropod fauna with no particular group predominant. Corals are common and represent a reef structure probably less than 30 m in depth (Saunders et al., 1986).

Occurrence: Known only from the late Miocene and early Pliocene Cercado and Gurabo Formations of Rio Cana and its tributary Cañada de Zamba, Dominican Republic.

DISCUSSION

Although the development of a dorsal tubercle is widespread in Recent species of *Lobatus*, the occurrence of this feature in *L. vokesae* is one of the earliest examples within the genus. The function of the dorsal shell protuberance is almost certainly anti-predatory, with a primary role in helping the animal to right its shell after being turned over by predatory fish, crabs, and octopus (Berg, 1975). The large dorsal tubercle forces the overturned shell to lean to either side, which reduces the time and extent to which the animal must extend its soft foot outward and unprotected to right the shell (Savazzi, 1991; see also Carefoot and Donovan, 1995). Selection for a prominent dorsal tubercle should be greatest in larger strombs with a flaring lip, and *L. vokesae* was one of the largest early strombs. Berg (1975) demonstrated that larger strombids are exposed for a longer period of time during righting due, in part, to their own weight and the broad, heavy lip.

Interestingly, the presence or absence of the dorsal tubercle varies interspecifically as well as intraspecifically in strombids, e.g., *Persististrombus granulatus* (Swainson, 1822). An example of the variability of shoulder knobs within a single species of *Lobatus* is illustrated by the case of *L. fetus* (Jung & Heitz, 2001), described from the late Pliocene Escudo de Veraguas Formation, Bocas del Toro area of Panama. In our opinion this is based on a specimen of *L. raninus* in

which the large dorsal shoulder knob is not developed. This variability can also be observed today, albeit uncommonly, in Recent specimens (Gijs Kronenberg, personal observation) and in Pleistocene fossil and Recent *L. costatus* (Gregory Herbert, personal observation). Therefore, a division of *Lobatus* into subgenera based solely on this sculptural element is unwarranted.

The Plio-Pleistocene radiation of *Lobatus* species in Florida resulted in a cohort of species that all had weaker tubercles than the fossil *L. vokesae* and living *L. costatus* or *L. raninus*, or had lost them altogether as in the cases of *Strombus* (*Macrostrombus*) *hertweckorum* Petuch, 1991 and *Strombus* (*Macrostrombus*) *leidyi* Heilprin 1886. Whatever changes in predatory patterns led to the loss of tubercles in the Floridian assemblages seem to have affected strombs as a whole, as the genus *Strombus* (s.s.), which is also greatly diversified in the Plio-Pleistocene of Florida, shows a similar pattern, with a radiation of Pliocene species with no tubercles on the last whorl (see Petuch, 1994; Hargreaves, 1995). The actual number of species within this radiation cannot be commented with certainty at present, as the numerous taxa described and illustrated by Petuch (1994) require revision.

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First Record of the Northeastern Pacific Patellogastropod Genus *Acmaea* from the Miocene of Japan and Its Paleobiogeographic Implications

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Abstract. *Acmaea mitra* Rathke, 1833 is the sole species of the genus *Acmaea* and inhabits lower intertidal to subtidal rocky shores in the eastern side of the North Pacific Ocean from California to the Aleutian Islands. The discovery of *Acmaea mitra* from the Upper Miocene of central Japan represents the first fossil record of the species and genus in the western side of the North Pacific and the oldest record of the genus *Acmaea*. The Late Miocene specimens are definitely referred to *Acmaea mitra* on the basis of overall shell morphology and shell microstructure. The fossil records strongly suggest that *A. mitra* became regionally extinct in the western side of the North Pacific by the end of the Late Miocene. *A. mitra* represents a good additional example of northeastern Pacific restriction, an uncommon biogeographic distribution pattern of marine organisms in the middle-latitude North Pacific Ocean during the late Cenozoic. The causes of the regional extinction of *A. mitra* in the western side of the North Pacific remain uncertain.

INTRODUCTION

Both the western side of the North Pacific (WSNP) and the eastern side of the North Pacific (ESNP) have well-documented fossil records of Cenozoic marine mollusks that provide basic data for examining the historical development of marine biogeography in this bioprovince. An interesting distribution pattern seen in fossil and modern mollusks in this bioprovince is geographic restriction: taxa living on both sides of the North Pacific during the Neogene subsequently became restricted either to the WSNP (the northwestern Pacific restriction) or the ESNP (the northeastern Pacific restriction). Vermeij (1989) surveyed historical biogeographic patterns of cool-temperate mollusks during the Neogene and recognized 15 taxa that reflected the northwestern Pacific restriction. On the other hand, he recognized only a possible case of the northeastern Pacific restriction. Later, Amano (1998) and Kurihara (2007) added several taxa reflecting this pattern. In these studies, the causes of regional extinction in the WSNP have not been examined rigorously. In this study, we present another case of northeastern Pacific restriction recognized in the patellogastropod limpet genus *Acmaea*.

The genus *Acmaea* accommodates only the single species *Acmaea mitra* Rathke, 1833. Many species once allocated to *Acmaea* in the North Pacific have now been referred to other genera of Lottiidae (e.g.,

Lindberg, 1981, 1986; Sasaki, 1999), and those fossil species described as *Acmaea* were based solely on shell morphology, a highly convergent character among patellogastropods, so that they need further study for reliable generic allocation. *A. mitra* inhabits hard substrates from the low intertidal to a depth of 30 m along the ESNP and the eastern Aleutian Islands (Lindberg, 1981). The discovery of *A. mitra* from the Upper Miocene of Japan reported in this paper is twofold: (1) the fossil record of the genus *Acmaea* extends back to the Late Miocene, and (2) it shows regional extinction of *A. mitra* in the WSNP by the end of the Late Miocene.

The following institutional abbreviations are used: GMNH (Gunma Museum of Natural History, Tomioka, Gunma, Japan), NSM (National Museum of Nature and Science, Tokyo; formerly National Science Museum, Tokyo, Japan), SDSNH (San Diego Natural History Museum, California, U.S.A.) and UMUT (University Museum, the University of Tokyo, Japan).

STRATIGRAPHY AND ASSOCIATED FAUNA

The three *Acmaea* specimens described in this paper are found in the molluscan fossil collection of GMNH (PI2258–2260). They were collected at locality HN08 [= locality C of Kato (2001)], a right bank of the Usui River, Minakuchi, Annaka City, Gunma Prefecture

(36°19'11"N, 138°53'12"E) in a fossiliferous pebbly medium- to coarse-grained sandstone bed in the lower part of the Itahana Formation. The Itahana Formation is the uppermost regressive unit of the Miocene Annaka Group (Takahashi & Hayashi, 2004), and is stratigraphically divided into the lower marine and upper non-marine units (Oishi & Takahashi, 1990). Based on the radiometric and biochronologic analyses of the underlying Haraichi Formation, Takahashi & Hayashi (2004) estimated the Itahana Formation as early Late Miocene age (ca. 11.0 Ma).

The lower unit of the Itahana Formation contains well-preserved marine mollusks of about 80 species (Kurihara, 2000). This assemblage is typical of Shiobara-type molluscan fauna (Iwasaki, 1970; Chinzei, 1978), Late Miocene temperate shallow-water associations characteristic in central and northern Honshu, Japan (Chinzei, 1986). Mollusks associated with *Acmaea* occupied various shallow marine habitats and include species of the gastropods *Charonia*, *Chlorostoma* and *Kelletia* indicative of temperate, subtidal rocky shores.

SYSTEMATIC PALEONTOLOGY

Order PATELLOGASTROPODA Lindberg,
1986

Superfamily PATELLOIDEA Rafinesque, 1815

Family LOTTIIDAE Gray, 1840

Genus *Acmaea* Eschscholtz in Rathke, 1833

Type species: *Acmaea mitra* Rathke, 1833, subsequent designation by Dall, 1871.

Discussion: Lindberg (1986) revised familial and generic level classification of species traditionally assigned to "Acmaeidae." Major changes in his classification are subdivision of "Acmaeidae" into Acmaeidae and Lottiidae and the restricted usage of Acmaeidae to a small monophyletic group that includes the monotypic, shallow-water genus *Acmaea* and the deep-water genus *Pectinodonta*. The members of this group share three pairs of uniform lateral teeth arranged in a posteriorly diverging inverted V-shape, identical ventral plate morphology, an absence of marginal teeth, similar gross anatomy and the same shell structure belonging to MacClintock's (1967) shell structure group 15 (Lindberg, 1986). However, Nakano & Ozawa (2004) recently demonstrated that *A. mitra* and *Niveotectura pallida* (Gould, 1859) constitute a monophyletic group on the basis of molecular data and similarity of radula, and also that *Pectinodonta* is clearly unrelated to *A. mitra*. Nakano & Ozawa (2007) classified *A. mitra* and *V. pallida* as a clade within Lottiidae and regarded

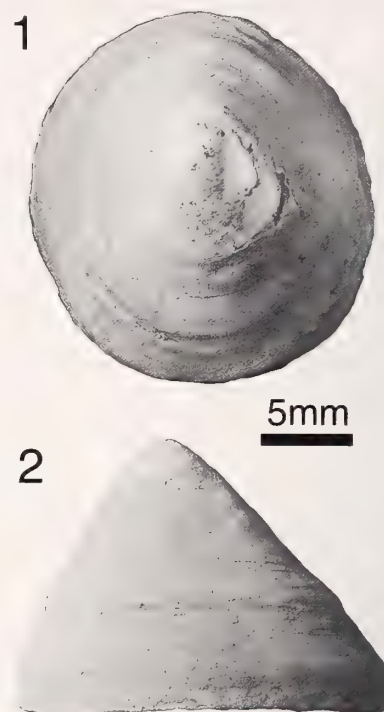


Figure 1. 1, 2, *Acmaea mitra* Rathke from the Upper Miocene Itahana Formation, apical and lateral views, GMNH PI2258, locality HN08, length, 21.0 mm, width, 19.0 mm, height, 15.3 mm.

Acmaeidae as a junior synonym of Lottiidae. The validity of this new systematic change needs to be confirmed by rigorous anatomical study because *A. mitra* and *N. pallida* belong to different shell structure groups and the anatomy of *A. mitra* has never been studied (Fuchigami & Sasaki, 2005). In this paper, we follow the classification proposed by Nakano & Ozawa (2007) for the familial assignment of *Acmaea*.

Acmaea mitra Rathke, 1833

(Figures 1, 2)

Acmaea mitra RATHKE IN ESCHSCHOLTZ, 1833, p. 18, pl. 23, fig. 4; ABBOTT, 1974, p. 29, fig. 145; LINDBERG, 1981, p. 63, fig. 64; LINDBERG & MARINCOVICH, 1986, fig. 2h; LINDBERG, 1988a, fig. 6d.

Description: Shell up to 21.0 mm in length, high conical, moderately thick, cap-shaped, with height about 3/4 of major apertural diameter. Apex in anterior 2/5, not curved anteriorly. Aperture subcircular, with length/width ratio 1.23. Anterior slope very weakly convex and other slopes almost straight. Surface devoid of any sculpture except for some concentric, knobby bulges indicative of growth halts, and concentric

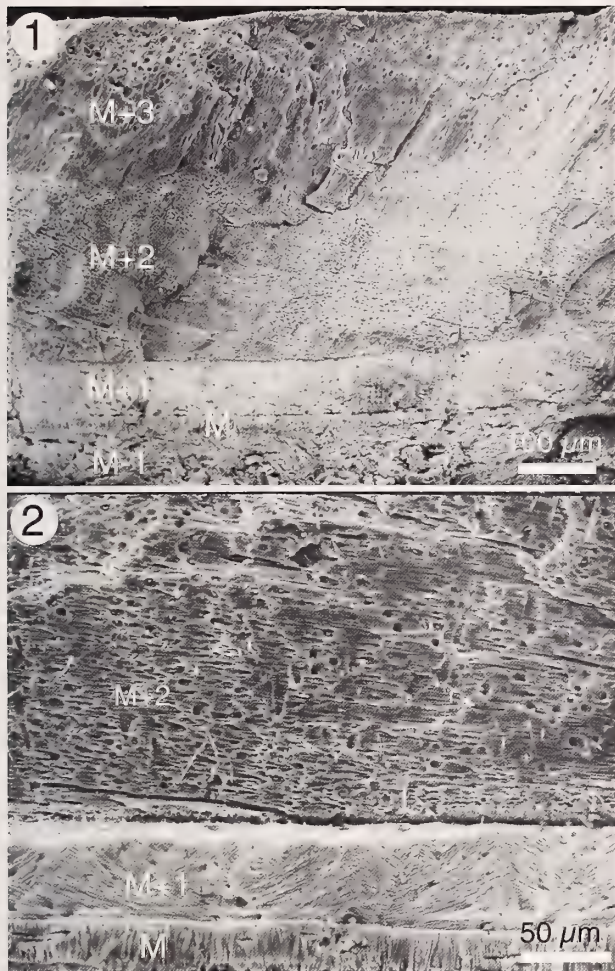


Figure 2. SEM micrographs of the shell walls in *Acmaea mitra* Rathke from the Itahana Formation, GMNH PI2259, locality HN08, etched by 1% HCl for 30 sec. 1, fractured section cut almost radially from the apex to shell margin showing the outermost complex prismatic layer (M+3), followed by the foliate layer (M+2), outer concentric crossed-lamellar layer (M+1), myostracum layer (M) and inner radial crossed-lamellar layer (M-1); 2, polished surface cut almost commarginally showing the foliate layer (M+2), followed by the outer concentric crossed-lamellar layer (M+1) and myostracum layer (M).

growth lamellae. Shell consists of five layers; outermost layer (M+3) of complex prismatic structure, followed by foliate layer (M+2), concentric crossed-lamellar layer (M+1), myostracum (M), radial crossed-lamellar layer (M-1).

Discussion: The suprageneric classification of living patellogastropods is primarily based on radular, gill and other anatomical characters, not preserved in fossil shells. However, shell morphology frequently exhibits convergence and parallelism, which makes the generic classification difficult. Analysis of shell microstructures

is a powerful method for classification of fossil species (e.g., Lindberg & Hickman, 1986; Lindberg, 1988a, b; Lindberg & Marinovich, 1988; Lindberg & Squires, 1990; Kase, 1994; Kase & Shigeta, 1996; Lindberg & Hedegaard, 1996). Patellogastropod shells consist of four to six successive layers including the myostracum, and each layer is composed of one of four basic microstructures (prismatic, foliated, crossed, and complex crossed) and also of either a microstructure different from adjacent layers, or, where the structure is the same, the two layer's major structural elements are oriented perpendicular to each other (MacClintock, 1967). This study demonstrated a general consistency between the classification based on soft anatomy and shell structure (MacClintock, 1967), who recognized 17 shell structure groups within the Patellogastropoda. Recently, Fuchigami & Sasaki (2005) added some deep-sea taxa recently accessible by submersible vessels and recognized 20 shell structure groups. They further emphasized the general, but not complete, consistency between the soft anatomy and shell structure. Among the 20 shell structure groups recognized by Fuchigami & Sasaki (2005), the specimens described here belong to their shell structure group P, diagnosed by an outermost irregular spherulitic prismatic layer, followed by a concentric regular foliated layer, concentrically arranged crossed-lamellar layer, the myostracum, and an inner radially arranged crossed-lamellar layer, clearly demonstrating allocation to the genus *Acmaea*.

The Late Miocene specimens from the Itahana Formation do not exhibit any difference in overall shell morphology from those of the modern specimens of *Acmaea mitra*. The periodic concentric and knobby bulges are seen both in the fossil and modern specimens. The largest specimen from the Itahana is slightly smaller than the common adult size of the modern specimens, but it appears not to be an important distinguishing character.

Acmaea sookensis Clark & Arnold (1923) from the Upper Oligocene Sooke Formation of Vancouver Island, British Columbia, Canada is the only fossil form that is sculptured only by concentric and periodic increments similar to those of the present species. This species, however, was reassigned to the genus *Patelloida* by Lindberg & Marinovich (1988) and therefore their resemblance is only superficial.

Distribution: *A. mitra* inhabits hard substrates of the low intertidal to a depth of 30 m along the Pacific side of North America from the warm-temperate sea of Isla San Martin, Baja California, Mexico (30°30'N) in the south to the cool-temperate sea of Umnak Island, eastern Aleutian Islands, Alaska (53°N) to the north (Lindberg, 1981; Vermeij et al., 1990). Recently, Golikov et al. (2001) recorded this species from the Sea of Okhotsk for the first time, but this record is

Table 1

Comparisons of shell and radular characters, habitat and feeding between *Acmaea mitra* and *Niveotectura pallida*.

	<i>Acmaea mitra</i>	<i>Niveotectura pallida</i>
Shell		
Color	White ¹	White ²
Maximum diameter	ca. 30 mm ¹	ca. 60 mm ²
Profile	High ¹	High ²
	Subcentral ¹	Subcentral ²
Structure group	Group P ³	Group C ³
Sculpture	Concentric growth lines ¹	Radial ribs and concentric growth lines ²
Radula formula	0-3-0-3-0 ¹	0-3-0-3-0 ⁴
Habitat		
Substratum	Hard bottom ¹	Hard bottom ²
Bathymetric range	Lower intertidal to 30 m ¹	Lower intertidal to 70 m ⁵
Geographic range	Aleutians to Baja California ¹	Sakhalin and Kuriles to central Japan, Korea, Maritime Territory ²
Food	Coralline algae ⁶	Coralline algae ⁷

References: ¹Lindberg (1981); ²Sasaki (2000); ³Fuchigami & Sasaki (2005); ⁴Sasaki (1998); ⁵Sasaki (2006); ⁶Padilla (1985); ⁷Fujita (1992).

based on the misidentification of *Erginus moskalevi* (Golikov and Kussakin, 1972) (B. Sirenko, pers. comm.). Therefore, the geographic distribution of this species is currently restricted to the eastern North Pacific.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Acmaea mitra is a subtidal species widely distributed along the ESNP from California to the eastern Aleutian Islands (Lindberg, 1981). In contrast, the fossil record of the genus *Acmaea* is represented only by *A. mitra* and was considered restricted to the ESNP. *A. mitra* occurs in the Pleistocene deposits of California (Grant & Gale, 1931; Valentine, 1961; Marincovich, 1976), and its oldest form is a well-preserved specimen (SDSNH 24351) from the lower part of the San Diego Formation of California, which is dated as middle Pliocene (ca. 3.5 Ma; T. A. Deméré, pers. comm.). Putative oldest forms of *Acmaea* in the ESNP are *Acmaea clarki* Van Winkle (1918) from the Oligocene of Washington and *Acmaea*? cf. *A. mitra* in the faunal list of the Upper Miocene Towsley Formation, the Ventura Basin of California (Winterer & Durham, 1962), but their identification cannot be confirmed because both species have never been studied rigorously. Therefore, the Late Miocene specimens in Japan represent the oldest fossil record and the first occurrence in the WSNP of this unique genus and species, and the most parsimonious view is that *A. mitra* originated in the WSNP during the Late Miocene and later migrated to the ESNP.

On the other hand, there is no reported occurrence of *A. mitra* in the Pliocene and Pleistocene of Japan, in spite of the presence of many fossiliferous localities yielding patellogastropod limpets as stated below. This

strongly suggests that *A. mitra* in the WSNP might have become extinct by the end of the Miocene. Vermeij (1989) discussed the origins of various biogeographic patterns seen today among late Neogene cool-water marine mollusks in the North Pacific and North Atlantic. The distribution pattern of *A. mitra* can be categorized into his "northeastern Pacific restriction," where species previously with an amphipacific distribution have become restricted to the ESNP. Molluscan taxa showing this distribution pattern include the lucinid bivalve *Epilucina californica* (Conrad, 1837), the venerid bivalves *Humilaria* Grant & Gale, 1931 and *Compsomyax* Stewart, 1930, the myid bivalve *Platyodon* Conrad, 1837, and the muricid gastropod *Nucella shiwa* (Chinzei, 1961) (Amano, 1998; Kurihara, 2007). As far as we are aware, the following genera can be added to the northeastern Pacific restriction taxa: the turrid gastropod *Megasurcula* Casey, 1904 and the cymatiid gastropod *Mediargo* Terry, 1968. *Megasurcula* is still extant in the ESNP, but in the WSNP this genus became extinct by the end of the Late Miocene (Oyama, 1954). *Mediargo* became extinct by the Pliocene in the ESNP, whereas it persisted only until the end of the Late Miocene in the WSNP (Smith, 1970). From the biostratigraphic point of view, the majority of cool- and mild-temperate marine molluscan clades in Japan range from the Late Miocene to Pliocene, suggesting that only a few clades became extinct during the Late Miocene. Aside from *Acmaea*, *Megasurcula* and *Mediargo*, the only molluscan groups extinct during the Late Miocene are the pectinid genera *Nanaoachlamys* Hatai & Masuda, 1953 and *Miyagipecten* Masuda, 1952 (Masuda, 1986; Matsubara, 1996).

Patterns of geographical restriction provide a clue for understanding the causes of extinction. If a species

persisted in one area while it disappeared in another, the possible causes of extinction can be attributed to the factors or events by which the two areas differ (Vermeij, 1989). Similarly, if a species disappeared in one area while its close relative persisted in the same area, the possible causes of extinction can be attributed to the factors by which the two species differ. *A. mitra*, now restricted to the ESNP, occupies the same habitat with, and is the closest relative to *N. pallida*, which is restricted to the WSNP (Nakano & Ozawa, 2004). Although these two species belong to different shell structure groups and have different external sculpture, they are almost identical in shell form and color, radular morphology, and feeding strategy (Table 1). Therefore, both *A. mitra* and *N. pallida* are regarded as ecological counterparts and may have responded similarly to changing environments in the geological past.

We undertook an extensive survey of the geographic and stratigraphic distributions of *N. pallida* in Japan (Figure 3). In this survey we treated *Niveotectura shigaramiensis* (Makiyama, 1927) as a junior synonym of *N. pallida*. Miocene specimens assignable to *N. pallida* are from the Ginzan Formation of Yamagata Prefecture (Nomura & Zinbo, 1937; NSM PM18322) and the Koshitomaezawa Formation of Iwate Prefecture (NSM PM17596), both in northeast Honshu. The Ginzan Formation has been dated as the late Middle Miocene by planktonic foraminifera and diatom biostratigraphy (Sato, 1986), and the Koshitomaezawa Formation as the Middle Miocene or the early Late Miocene based upon radiometric dating of its overlying unit (Suto & Ishii, 1987). The shell of the Ginzan specimen consists of a thick, outer complex prismatic layer and a thin, inner concentric crossed-lamellar layer that belongs to Fuchigami & Sasaki's (2005) Group P as does the modern *N. pallida*. The specimen described by Yokoyama (1925b) from Sakae in Nagano Prefecture, which Marincovich & Lindberg (1988) regarded as from the Upper Miocene Ogawa Formation, is now believed to be from the Lower Pliocene Shigarami Formation (e.g., Amano & Koike, 1993). Lindberg & Marincovich (1988) noted that the oldest example of *N. pallida* was from the Joban coalfield of northeast Honshu, Japan. Yokoyama (1925a) recorded *N. pallida* from three localities in the Joban coalfield, of which Yunami (Tozenji) is known as a classic (now destroyed) fossil locality of the lower Middle Miocene Kokozura Formation of the Takaku Group (Yanagisawa, 1996). If the occurrence of *N. pallida* from Yunami is correct, it represents the oldest form of this species. However, we cannot confirm Yokoyama's (1925a) record because the specimen of *N. pallida* from Yunami was not illustrated by him and has not been found in the UMUT collection. Therefore, we excluded the occurrence from Yunami in this discussion. The Pliocene and

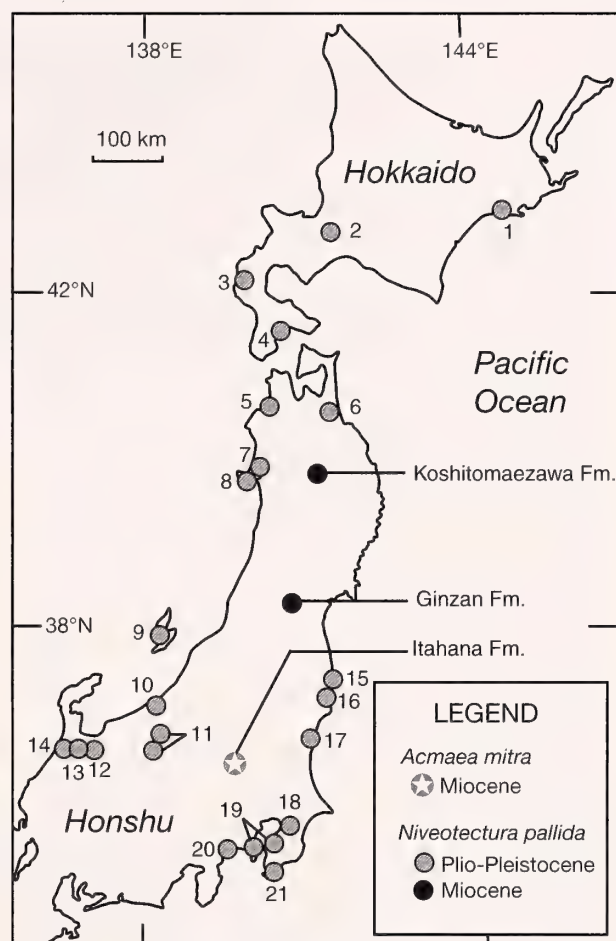


Figure 3. Geographic and stratigraphic distribution of fossil *Acmaea mitra* and *Niveotectura pallida* in Japan. Sources of fossil records of *Niveotectura pallida* are as follows: 1, Otanoshike Fm. (Akamatsu, 1988); 2, Otoebetsugawa Fm. (Akamatsu, 1987); 3, Setana Fm. (Suzuki, 2002, 2003); 4, Tomikawa Fm. (Sakagami et al., 1966); 5, Narusawa Fm. (Iwai, 1960); 6, Noheji Fm. (Iwai and Siobara, 1969); 7, Sasaoka Fm. (Nomura and Hatai, 1938); 8, Shibikawa and Katanishi Fms. (Ogasawara et al., 1986); 9, Sawane Fm. (Yokoyama, 1926; Omori, 1977); 10, Tanihama Fm. (Amano et al., 1987); 11, Shigarami Fm. (Yokoyama, 1925b; Makiyama, 1927; Nagamori, 1998); 12, Mita Fm. (Fujii and Shimizu, 1991); 13, Zukawa Fm. (Fujii and Shimizu, 1992); 14, Omma Fm. (Yokoyama, 1927; Kaseno and Matsuura, 1965; Matsuura, 1985); 15, Tomioka Fm. [= Dainenji Fm.] (Nemoto and O'Hara, 2005); 16, Taga Group [= Dainenji Fm.] (Nemoto and O'Hara, 1979); 17, Hitachi Fm. (Yokoyama, 1925a; Noda et al., 1995); 18, Shimosa Group (Yokoyama, 1922; O'Hara, 1982); 19, Kazusa Group (Yokoyama, 1920; Shikama and Masujima, 1969; Baba, 1990); 20, Ninomiya Group (Okumura, 1980); 21, Toyofusa Fm. (Baba, 1990). Records from the Kazusa and Shimosa Groups are too numerous, so some representative works are cited.

Table 2

Ranges of monthly mean sea surface temperature (SST) near the southern and northern distribution limits of *Acmaea mitra* and *Niveotectura pallida* in the North Pacific.

Locations	Monthly mean SST ranges (°C)	Remarks
Jueau, Alaska	2.2–10.6 ¹	Northern limit of <i>A. mitra</i>
Newport Beach, California	14.1–21.1 ¹	Southern limit of <i>A. mitra</i>
Akkeshi, Hokkaido	0.7–19.1 ²	Northern limit of <i>N. pallida</i>
Isozaki, Ibaraki	9.1–21.2 ²	Southern limit of <i>N. pallida</i>

References: ¹U.S. National Oceanographic Center (2006); ²Japan Oceanographic Data Center (2007).

Pleistocene occurrences of *N. pallida*, in contrast, are abundant and distributed widely in central and northern Japan as shown in Figure 3.

The fossil record mentioned above indicates that both *A. mitra* and *N. pallida* lived in the WSNP during the Late Miocene, and that *A. mitra* became extinct there by the end of the Late Miocene whereas *N. pallida* persists today. Vermeij (1989) hypothesized five major causes that governed the extinction for Neogene marine invertebrates in the North Atlantic and North Pacific: (1) anoxia; (2) regression and habitat loss; (3) reduction in primary productivity; (4) competition and predation; and (5) cooling and warming. The first and second hypotheses are very unlikely because *A. mitra* inhabited upper subtidal rocky shores where anoxia and habitat loss may hardly have occurred. The third hypothesis has been recognized as a cause of extinction for many Neogene mollusks in the western tropical Atlantic and the eastern temperate North Pacific (see Vermeij, 2001 for review). Vermeij (1989) found that large suspension-feeding bivalves in the ESNP became extinct more than those in the WSNP during the Pliocene, and suggested that reduction or interruption of primary productivity was a possible cause of this extinction in the ESNP. This hypothesis evidently contradicts the distribution pattern of *A. mitra*. The fourth hypothesis—predation and competition as agents of extinction—is well known to be possible causes of extinction for terrestrial organisms but no convincing example has been proposed for marine organisms (Vermeij, 1987, 1989, 2004).

The last hypothesis, especially cooling, seems to be the most plausible for the regional extinction of amphipacific marine biota in the WSNP, because the cool-temperate WSNP shows wider annual temperature fluctuations than the ESNP with extensive development of winter ice (Vermeij, 1978, 1989). However, this hypothesis is unlikely for the selective extinction of *A. mitra* from the WSNP because this species has wide temperature tolerances the same as *N. pallida* in modern seas. The available monthly mean sea surface temperature near the northern- and southernmost distribution areas of *A. mitra* and *N. pallida* are almost the same (*A. mitra*, 2.1–21.1°C; *N. pallida*, 0.7–21.2°C;

Table 2). If *A. mitra* in the WSNP had become extinct by cooling or warming, *N. pallida* would have also become extinct at the same time. In the WSNP, cooling and warming events occurred at the latest Miocene (ca. 6–5 Ma) and the Early Pliocene (ca. 5–4 Ma), respectively (e.g., Ogasawara, 1994; Suzuki & Akamatsu, 1994), but *N. pallida* survived even under these paleoclimatic conditions. G. J. Vermeij (pers. comm.) suggested that cooling is still a possible cause of the regional extinction of *A. mitra* from the WSNP if this species had a limited geographic range during the Late Miocene in the WSNP: such a small population(s) might have been affected by the environmental deterioration more severely than widely distributed species. However, the poor fossil record of *A. mitra* and *N. pallida* during the Late Miocene does not allow us to justify this possibility.

In summary, any major hypotheses previously proposed cannot interpret explicitly the development of the unique distribution pattern shown here in *A. mitra*. However, documentation and accumulation of such examples may contribute toward further understanding of the origin of various distribution patterns of marine organisms in the North Pacific.

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A New *Phaenomenella* Fraussen & Hadorn, 2006 (Gastropoda: Buccinidae), from the Andaman Sea

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Abstract. A peculiar species from the Andaman Sea is described as *Phaenomenella mokenorum* sp. nov. The generic placement is based on conchological characteristics of the apical whorls, sculpture and columella. The new species differs from its congeners *Ph. inflata* (Shikama, 1971), *Ph. insulapratasensis* (Okutani & Lan, 1994) and *Ph. angusta* Fraussen & Hadorn, 2006 by having smoother sculpture and a distinct shape.

Key Words: Andaman Sea, Gastropoda, Buccinidae, *Phaenomenella*, new taxon

INTRODUCTION

The genus *Phaenomenella* Fraussen & Hadorn, 2006 is characterized by the angular shape of the apical whorls. Two species, *Phaenomenella inflata* (Shikama, 1971) and *Phaenomenella angusta* Fraussen & Hadorn, 2006, are known from the East China Sea and off Taiwan. One species, *Phaenomenella insulapratasensis* (Okutani & Lan, 1994), is known from the South China Sea. The new species here described is from the Andaman Sea, hereby extending the range of the genus into the eastern Indian Ocean.

The material reported on in the present study originates from the International Indian Ocean Expedition 'ANTON BRUUN' conducted in 1963.

Abbreviations:

ANSP	Academy of Natural Science, Philadelphia, U.S.A.
KF	collection Koen Fraussen, Aarschot, Belgium
MNHN	Muséum national d'Histoire naturelle, Paris, France

SYSTEMATICS

BUCCINIDAE Rafinesque, 1815

Genus *Phaenomenella* Fraussen & Hadorn, 2006. Type species: *Manaria inflata* Shikama, 1971 (type locality: Taiwan) by original designation.

Phaenomenella mokenorum sp. nov.

Figs. 1–6

Type material: Holotype (55.6 mm) ANSP 291386,

paratype 1 (44.0 mm) and paratype 2 (35.4 mm) ANSP 416212 (from the type locality).

Paratype 3 (42.3 mm) and paratype 4 (40.2 mm) (Andaman Sea, southern Myanmar (Burma), west off Twin Island, ANTON BRUUN st. 22B, 10°39'N, 97°06'E, 274–293 m deep, on sand-mud, by dredge, 24/3/1963), ANSP 291928.

All shells empty or inhabited by hermit crab.

Type locality: Andaman Sea, Thailand, E-SE off Phuket Island, ANTON BRUUN stn 17, 07°40'N, 97°08'E, 512–503 m deep, on green-brown clay, by shrimp trawl, 21/3/1963.

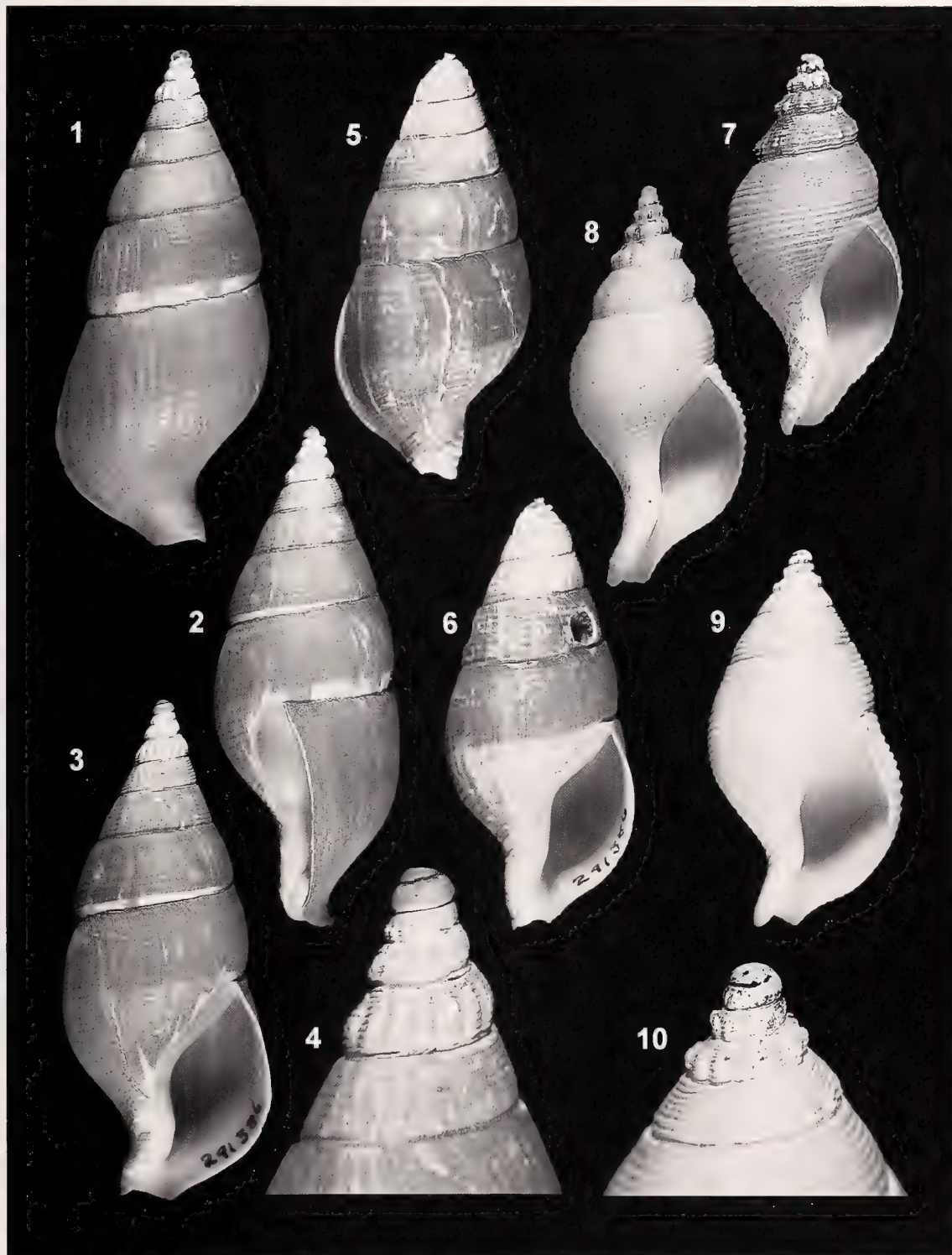
Range and habitat: Only known from the type material. Andaman Sea, off Thailand and off southern Myanmar.

Description: Shell large for the genus (up to 55.6 mm), thin but solid, color white to pale brownish, shape slender with moderately high spire, body whorl rather inflated with short siphonal canal.

Protoconch rather bulbous, 2.7 mm in diameter, damaged (holotype) or decollate (paratypes), the 2 remaining protoconch whorls are concave and smooth, last whorl slightly angulate below periphery. Transition to teleoconch indistinct.

Teleoconch whorls up to 7 in number, laterally flattened. Suture deep, abapically slightly truncate.

First 1 1/2 whorls eroded, traces of broad but low and smooth spiral cords occasionally visible, with a fine line as interspace. All following whorls with 10 spiral cords, flattened with shallow, narrow interspaces at second whorl. Spiral cords gradually becoming broader, lower and flattened towards penultimate whorl. Body whorl rather smooth, indistinct spiral cords. First 1 1/2 whorls eroded, traces of axial ribs occasionally appearing, last half of second whorl with 8 axial ribs,



Figures 1–10. 1–6. *Phaenomenella mokenorum* sp. nov. 1–4. 55.6 mm, holotype, Andaman Sea, Thailand, E-SE off Phuket Island, ANTON BRUUN stn 17, 07°40'N, 97°08'E, 512–503 m deep, ANSP 291386; 5–6. 44.0 mm, paratype 1, same locality, ANSP 416212. 7–8. *Phaenomenella inflata* (Shikama, 1971) 7. 30.5 mm, Taiwan, TAIWAN 2000, stn CP27, 22°13.3'N, 120°23.5'E, 326 m, MNHN; 8. 33.8 mm, off Suao, Taiwan, dredged, 190 m, KF nr. 0524. 9–10. *Phaenomenella insulapratensis* (Okutani & Lan, 1994), 39.2 mm, off Vietnam, trawled by Taiwanese fisherman, KF nr. 1495.

weak near both sutures, more prominent near periphery. Third whorl suddenly smooth, no traces of axial sculpture on subsequent whorls.

Aperture semi-oval. Columella strongly twisted, occasionally curved (paratypes), callus thin, smooth. Outer lip thin or slightly thickened, occasionally slightly curled outwards (paratype 1). Outer lip smooth (paratype 1) or with weak traces of internal lirae (holotype), occasionally with 17 or 19 internal lirae (paratypes 3–4). Siphonal canal short, broad, open.

Periostracum greenish brown, well adherent, velvety with numerous fine, rather straight (only weakly curved) incremental lamellae running from suture to suture when fresh (holotype), smooth and glossy when eroded (paratype 1).

Animal and radula unknown.

Remarks: *Phaenomenella mokenorum* sp. nov. is characterized by the elegant shape (slender spire in combination with convex body whorl) and the spiral sculpture of equal strength elements.

The generic placement is based on morphological similarities of the distinctive shape of the apical whorls (strongly angular), sculpture and columellar shape, which are all typical for the genus.

Phaenomenella inflata from off Taiwan differs by having more convex whorls and a shorter spire in combination with a longer siphonal canal.

Phaenomenella insulapratasensis from off Vietnam

differs by having a more ovoid shape, a shorter spire, a more solid shell and a smaller adult size.

Phaenomenella angusta from off Taiwan and southern Japan differs by having a more slender shape with a higher spire and a sharper spiral sculpture.

Etymology: *Phaenomenella mokenorum* sp. nov. is named after the moken, sea-nomads, the indigenous people of the region.

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Development of *Tyrodina fungina* Gabb, 1865 (Gastropoda: Notaspidea) from the Pacific Coast of Panama

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Abstract. The biology of notaspidean gastropods is not well studied and the development of tyrodinoids is almost entirely unknown. Here I report observations on the reproduction and development of *Tyrodina fungina* (Gabb, 1865) from the Perlas Islands on the Pacific coast of Panama. This species lives, feeds, and lays flat egg ribbons on the verongid sponge *Suberea azteca* (Gómez and Bakus, 1992). The egg ribbons contain hundreds of rows of 80 μm eggs, each singly encapsulated in a round 125 μm capsule. The ribbon also includes strings of extra-capsular material which is unevenly distributed through the mass. The eggs have equal cleavage and the ciliated “trochophore” stage is followed by an encapsulated veliger, which has a large, dark-red pigmented mantle organ. At hatching the transparent, left-handed larval shell is 123 μm long, and each semicircular velar lobe is unpigmented. There is a distinct operculum, but the eyes and tentacles have not developed. After 3 weeks in culture the larvae had reached a shell length of 162 μm and still had no eyes or tentacles. The larvae did not survive to settlement.

Key Words: Tyrodinidae, Notaspidea, extra-capsular yolk

INTRODUCTION

The opisthobranch superfamily, Tyrodinoidea, contains notaspideans with an external, limpet-like shell. The superfamily consists of 2 families, the Umbraculidae and the Tyrodinidae. Umbraculidae is monotypic with a single species with a worldwide distribution, and the Tyrodinidae is comprised of two genera; *Tyrodina* with 5 species and *Anidolyta* with 2 or possibly 3 species (Willan, 1987). *Tyrodina* is considered “primitive” in the notaspideans. However the monophyly of the notaspideans is contentious, with some families possibly including the sister-group of the nudibranchs (Wägele and Willan, 2000). Therefore data on any notaspideans could be useful in testing their monophyly as well as helping to reconstruct character state evolution within the opisthobranchs.

Although representatives of both families of tyrodinoids have been examined morphologically, the biology of most of the species remains largely unstudied and the life history is not known for any species of *Tyrodina* (Willan, 1998; Gibbson, 2003). One species each of the five described species of *Tyrodina* occurs in Australia, South Africa, the Mediterranean, western Atlantic, and Tropical East Pacific. This unusual biogeographic pattern and the fact that the species are diagnosed with few subtle anatomical features has lead to suggestions that all species of *Tyrodina* should be synonymized under the name *T. perversa* (Thompson,

1970). While disagreeing with this extreme view, Willan (1998) suggests that developmental data could be useful in further demonstrating the validity of the *Tyrodina* species.

The only published developmental information for the superfamily is limited to the following observations of *T. corticalis* and *Umbraculum sinicum*, each reported for a single spawn of a single female by Thompson (1970) and with some additional information from one other individual of *U. sinicum* from Ostergaard (1950). *Tyrodina corticalis* is reported to have a bright yellow spiral egg ribbon that is attached flat to the substrate and to contain eggs 98 μm in diameter. *Umbraculum sinicum* deposited a coiled ribbon that contained egg capsules 480–500 μm in diameter. Each capsule contained 30–45 eggs, which were 80–90 μm in diameter. Larvae hatched with statocysts and a distinct operculum but without eyes. A pigmented mantle organ is evident from Figure 32 in Ostergaard (1950). No other observations of the embryology or larval type have been published for the entire superfamily. Here I describe the embryology and larval development of *Tyrodina fungina* as a step towards documenting development in this phylogenetically important group.

MATERIALS AND METHODS

12 adult *Tyrodina fungina* were collected by dredging in the Perlas Islands (8°35.9'N, 78°1.0'W and 8°16.0N, 79°1.3W) during February and April 2007. The snails were brought to the surface attached to the host sponge

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Suberea azteca (Gómez and Bakus, 1992). *Tylodina fungina* is usually reported associated with *Aplysina fistularis*, which appears superficially similar to *S. azteca*. Identification of *S. azteca* was verified from a preparation of skeletal material and comparison with the original species description. The snails and some host sponge were kept in running seawater at ambient temperature (22–26°C). The sponge survived for 2 weeks under these conditions, but the snails survived for up to 6 weeks. Portions of egg ribbon were scraped from the surface of the containers and collected from the sponge skeletons and maintained in fingerbowls in the laboratory at 21–23°C. The water was changed daily and larvae were collected immediately upon hatching. After hatching the larvae were transferred to finger bowls with 1 µm filtered water. The water was changed every 2–3 days and larvae were fed *Isochrysis galbana*. The hydrophobic larvae were kept from getting stuck in the surface tension of the water by the addition of a few flakes of cetyl alcohol. Only uncleaved eggs and naturally hatched larvae were measured.

RESULTS

In the laboratory, the adult *Tylodina fungina* remained closely associated with the live sponge and were frequently observed feeding on it (Figure 1A). One of the sponges had been completely consumed by the snails and all that remained was the spongin skeleton. This skeleton was covered with egg ribbons (Figure 1B), giving the appearance of badly damaged sponge tissue when, actually, no sponge tissue remained on the skeleton. The three other sponges that remained largely intact showed eroded areas which each housed a snail (Figure 1A). Egg ribbons were not evident on these sponges, which suggests that egg production commences after depletion of the food supply. After the sponges died the snails deposited egg ribbons on the containers in which they were housed (Figure 1C).

The bright yellow egg ribbons were attached flat against the substrate and were arranged in an irregular spiral when laid on a smooth surface (Figure 1C). Those that were attached to the sponge skeleton were irregularly twined around the skeleton and incorporated portions of the skeletal fibers (Figure 2A). The 80.5 µm (n = 29, s. d. = 1.4 µm) eggs were yellowish cream-colored and were each contained within a 125.1 µm capsule (n = 19; s.d. 3.5 µm). These capsules are embedded in rows within the gel of the egg ribbon. Between the rows of egg capsules there were bright yellow streaks of extracapsular material (Figure 2 B–F). These streaks were inconsistent in width and were absent from some portions of the egg ribbon, but when present there tended to be 2 rows of eggs between each streak (Figure 2). At high magnification the streaks

Table 1

Developmental time table of *Tylodina fungina* at 21–24°C.

Time	Stage
24 hrs	Blastula
48 hrs	Gastrula
4 days	“Trochophore”
6 days	Shell begins to develop
7 days	PMO develops
13–15 days	Hatching

could be seen to consist of numerous tiny droplets (Figure 2F), which remained in the gel after hatching.

Several egg ribbons were collected prior to first cleavage and were observed until hatching. A developmental schedule is given in Table 1. The two polar bodies remain associated with the eggs at least until gastrulation (Figure 3D). The first two cleavages appear to be equal and synchronous and there is no polar lobe (Figure 3B, C). By the beginning of the third cleavage division, one of the 4 cells is already slightly ahead of the others. Later, cleavage becomes more asynchronous and eventually forms a compact, animal-vegetally flattened blastula (Figure 3D). The gastrula is horseshoe shaped and appears to have been formed at least partially by invagination (Figure 3E). A trochophore-like stage with a distinct raised ring of cilia around the anterior end (Figure 3F) follows gastrulation. The pre-hatching veliger shows a distinct foot with an operculum (Figure 3G) and pair of statocysts and a large, pigmented mantle organ (PMO) on the right side (Figure 3G, H). The PMO appears black with epi-illumination and is dark red under transmitted light.

At hatching the larvae have a round, transparent shell 123.1 µm (n = 58 from 3 ribbons; s. d. = 6.1) in length with a single slightly left-handed whorl. On living larvae the shell appears smooth, but slight granular sculpture is evident on dead shells. The velum is un-pigmented and consists of two small, equal, semicircular lobes (Figure 3H). The operculum is present and the foot is simple. After 3 weeks the larvae had grown to 161.8 µm (n = 7; s. d. = 8.3) but still had not developed eyes or tentacles and showed no signs of competency to settle. The larvae survived for at most 4 weeks in culture. Despite repeated attempts to culture them, it was not clear why they failed to thrive.

DISCUSSION

As previously noted by Robertson (1985), developmental features have the potential to contribute useful data to understand high-level gastropod relationships. The main drawback to using developmental features is

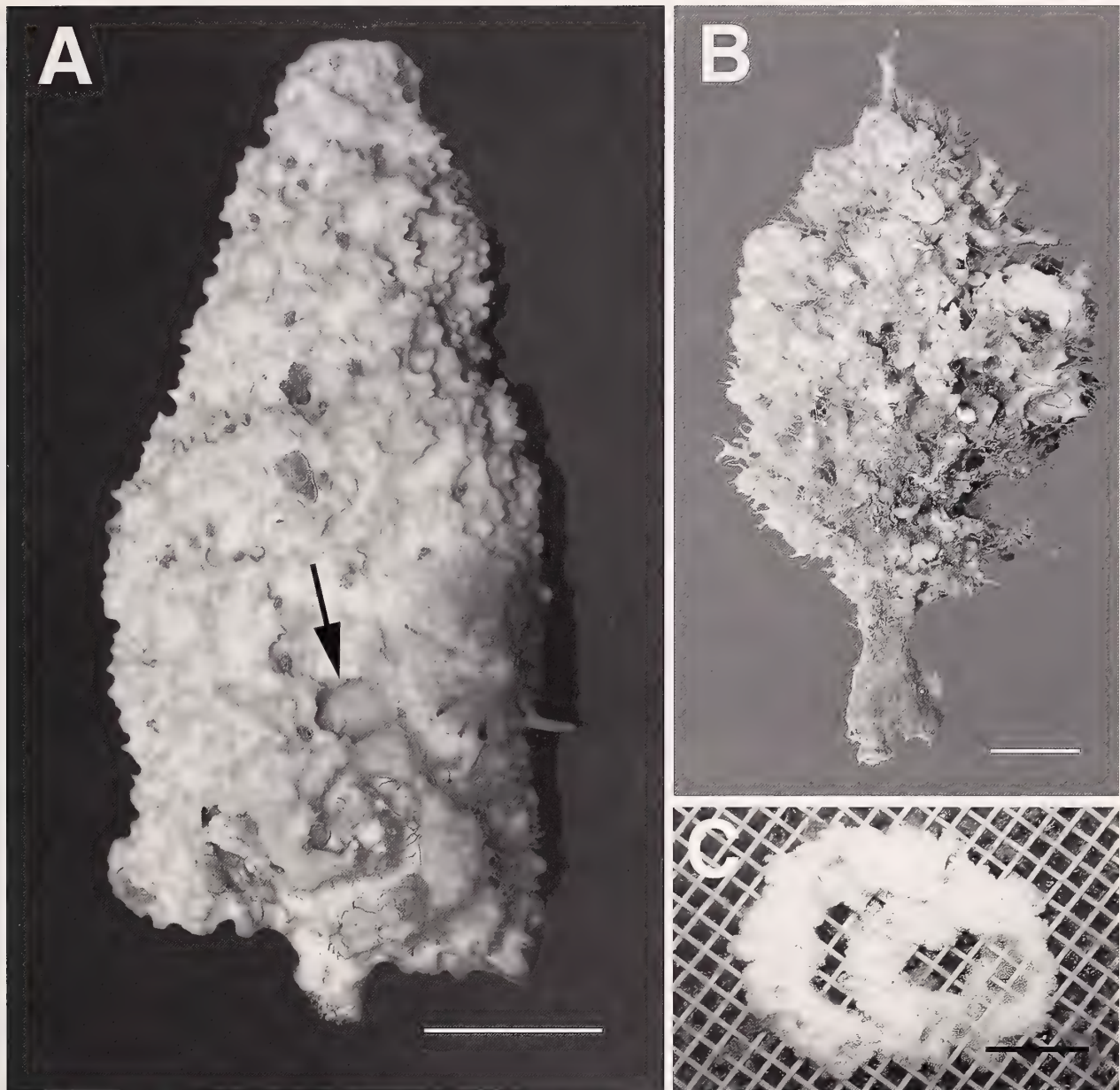


Figure 1. Adult *T. fungina* with host sponge and egg masses. **A.** Two adult *T. fungina* on their host sponge. The smaller individual (arrow) is sheltered in a depression in the ectosome of the sponge. Scale = 4 cm; **B.** Skeleton of the host sponge covered with egg masses of *T. fungina*. Scale = 2 cm; **C.** Egg mass of *T. fungina* deposited on a plastic mesh. This mass is smaller and more tightly coiled than most of the masses deposited on flat surfaces. Scale = 1 cm.

that few data are available for many interesting groups. Tylodinoids are a prime example of a phylogenetically important group where little is known. However, some comparisons of the egg masses can be made with previously published observations.

The egg masses of *T. fungina* as described here seem generally similar to those of the Australian congener, *T. corticalis*, with a flat ribbon attached in a coil to the substrate. Egg masses of both species are yellow, but

contain cream-colored eggs (Thompson, 1970), suggesting that *T. corticalis*, like *T. fungina*, deposits extracapsular material in the egg ribbons. The difference in egg size between the 80 μm eggs of *T. fungina* and the 98 μm eggs of *T. corticalis* further bolsters their status as distinct species. The lack of information on *Umbraculum* species makes it difficult to determine how consistent the egg masses are throughout the family. The large number of eggs per capsule in *Umbraculum*

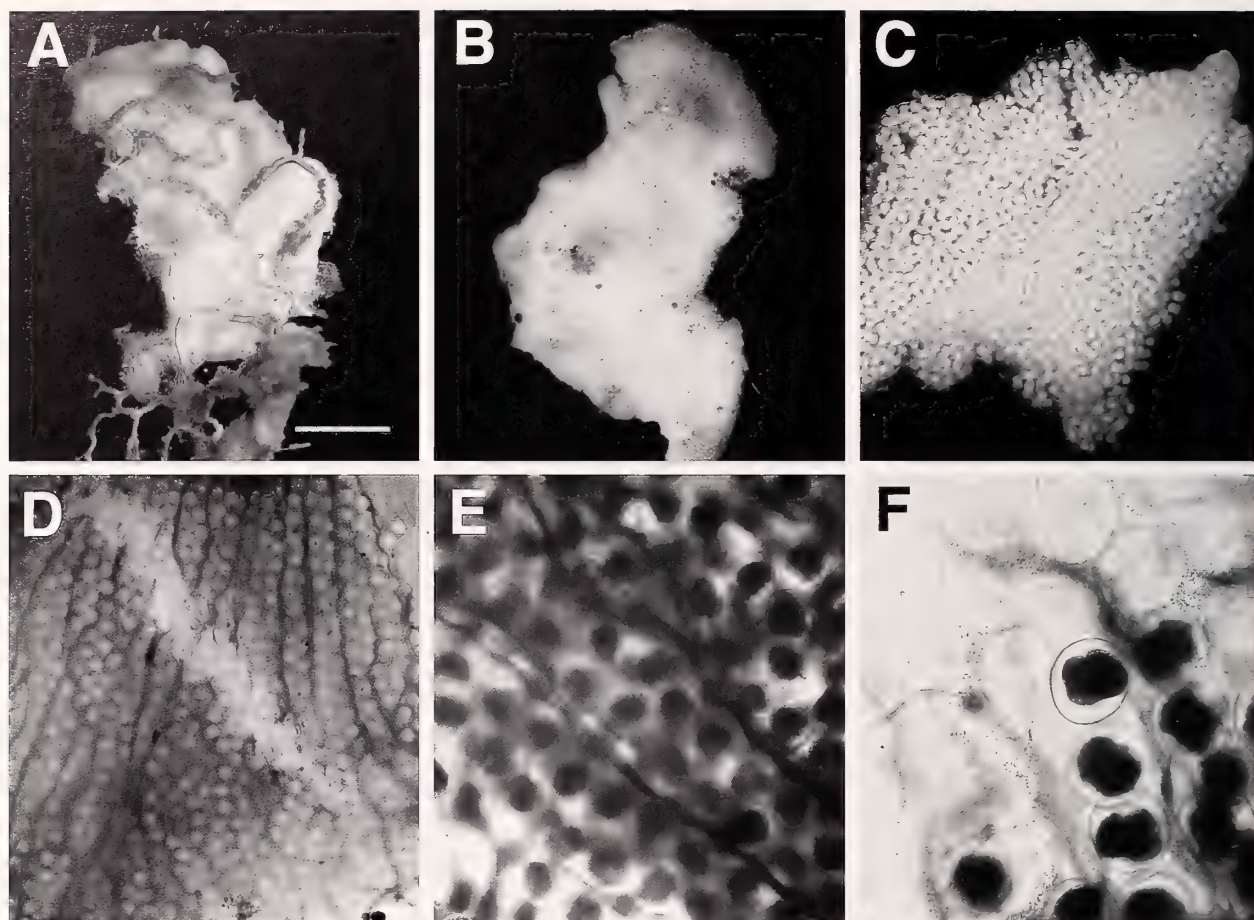


Figure 2. Egg ribbons of *T. fungina*. **A.** Egg ribbon attached to the sponge skeleton; Scale = 1 cm; **B.** Egg ribbon that was laid on a smooth surface, the lines of extra-capsular material are clearly visible in color but difficult to see in black and white. Scale = 1 cm; **C.** The multiple layers of eggs and the uneven distribution of the extracapsular material can be seen. Scale = 5 mm; **D.** and **E.** Closer views showing the arrangement of eggs in two rows between each string of opaque extracapsular material. Scale = 1.5 mm and 500 μ m respectively; **F.** Detailed view of egg capsules embedded in the gel and the droplets of extracapsular material. These droplets remain in the gel after hatching. Scale = 150 μ m.

sinicum (Thompson, 1970) does show that there are some differences.

Unlike the Tylodinoids, there is considerable published information on the development of the other notaspidean superfamily, the Pleurobranchioidea (reviewed in Gibson, 2003). Gibson (2003) described the typical features of notaspidean development on the basis of her detailed observations of the development of *Pleurobranchaea maculata* and a review of the literature. These new observations of *Tylodina* development suggest that tylodinid development may differ significantly from pleurobranchid development. Unlike pleurobranchids, tylodinids have a larval operculum and extracapsular material (Table 2). Unfortunately, the larvae in this study did not survive long enough to determine if the larval mantle overgrows the larval shell (an unusual characteristic of pleurobranchids). It is

unlikely, however, that this would happen as adult Tylodinids, unlike pleurobranchids, have a fairly large external shell that is not covered by the mantle. It may be that the mantle overgrowth of the larval shell is what prevents pleurobranchid larvae from being hydrophobic, like other opisthobranch veligers.

The most unusual characteristic of the *Tylodina fungina* egg masses was the presence of extracapsular material. Similar material in opisthobranch egg ribbons is usually referred to as "yolk" in the literature, although there is usually little evidence beyond a similar color that suggests this material is indeed yolk. "Yolk bodies" embedded in the egg ribbon jelly outside the egg capsules are well known for tropical chromodorids and sacoglossans (Boucher, 1983). Boucher (1983) described three kinds of extra-capsular material. Chromodorids have yolk that is present as either cap-

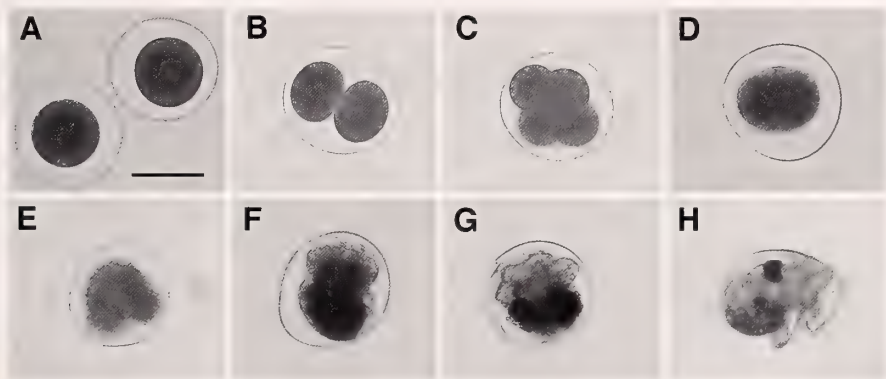


Figure 3. Developmental stages of *T. fungina*. **A.** Uncleaved eggs individually enclosed in transparent capsules, which have been removed from the gelatinous mass. **B.** 2-cell stage, the polar bodies are not visible. **C.** 4-cell stage. **D.** The flattened blastula with the polar bodies marking the animal pole. **E.** Horse-shoe shaped gastrula **F.** Late “trochophore” stage with the beginnings of the shell showing on the bottom right **G.** Encapsulated veliger, 2 days prior to hatching. The red PMO is visible on the animal’s right and has not yet developed the black pigmentation. The velum, foot, and operculum are all well developed. **H.** 2-week old veliger larva. Scale = 100 μm.

like “yolk bodies” associated with individual capsules or discrete “yolk” masses distributed through the egg mass. *Elysia* species have strings of “yolk” running through the egg masses (Boucher, 1983). The overall morphology of *Elysia* egg masses is strikingly similar to those described here for *T. fungina* (P. Krug, pers. com). It has yet to be determined if the material included in the *T. fungina* egg masses is yolk, but it seems unlikely. The material is a different color (bright yellow) from the eggs (cream) and remains in the gel of the egg mass after hatching. The presence of this “yolk” in several other species with planktotrophic development, where the larvae are not retained near the egg mass after hatching (Boucher, 1983) suggests that this material might not have a nutritive function. There

is some circumstantial evidence that the function in *Tylodina* might be defensive. Becerro et al. (2003) showed that egg masses and extracts of egg masses from *Tylodina perversa* deter feeding by damselfish with the same efficiency as the chemically defended adult snails and Ebel et al. (1999) showed that defensive chemicals are sequestered in the egg masses of the same species. Detailed examination of this material is necessary before their function can be determined.

Acknowledgments. I thank the captain and crew of the R/V Urraca without whom I would not have collected the samples, A. Baeza for photographing the adult animals, M. C. Diaz and R. Thacker for identifying the sponge, and the Autoridad Maritima de Panamá for issuing necessary permits to the Smithsonian Tropical Research Institute.

Table 2
Comparisons of Tylodinid and Pleurobranchid development.

Character	Tylodinids	Pleurobranchids
Egg masses	Flat ribbons	Strings
Extra-capsular material	Present	Absent
Extra-embryonic, intra-capsular yolk	Absent	Present sometimes
Type 1 larval shell	Present	Present
Larval Shell	Hydrophobic	Not hydrophobic in <i>Pleurobranchaea maculata</i> ‡
Larval shell growth	No observations of mantle-over growth *	Over-grown by mantle
Operculum	Present	Absent §
PMO	Present	Present
Larval eyes	Absent at hatching	Absent at hatching

‡ Glenys Gibson, pers. com. 2007
* More data is necessary to verify this observation.
§ Reported as absent in the group by Gibson (2003), but curiously Ostergaard (1950) reported opercula on 2 species of Pleurobranchids. Opercula were not present in other published studies of development in this group.

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BOOK REVIEW

The Recent Molluscan Fauna of Île Clipperton (Tropical Eastern Pacific)

by KIRSTIE L. KAISER. Festinus 39, Supplement. 162 pp.

The atoll of Clipperton is not only the most isolated island in the tropical eastern Pacific, but its marine fauna is a unique biogeographic mixture of species, with approximately equal parts arriving from the Indo-West Pacific and Panamic Provinces. Kirstie Kaiser's new volume on the molluscs of Clipperton is a substantial and welcome addition to the study of this little-known fauna. Some 285 molluscan species, including planktonic species and two terrestrial gastropods, are now known from the atoll, a huge increase from the 92 species recorded previously. The volume contains illustrations, details of collecting localities, a list of recorded species and their geographic distribution, and an account of rejected records.

A striking feature of this fauna is the large number of minute species, many of which probably have brief pelagic larval stages or none at all. Unfortunately, most of these taxa are identified only to genus or even family level, so that their phylogenetic and biogeographic affinities remain unknown.

Some major tropical groups are entirely absent in Clipperton's fauna. For example, there are no patello-gastropod limpets, turban snails (Turbininae), strombids, olives (Olividae), siphonariid (or pulmonate) limpets, cockles (Cardiidae), venerids, and tellinids. Although many of these groups comprise sand-dwellers, and sand is rare at Clipperton, some sand-dwelling gastropods do occur on the island, including a few cones, terebrids, moon snails (naticids), and a nassariid. These faunal peculiarities raise interesting questions that for the most part are neither posed nor discussed in this volume.

Taxonomic remarks are given for some species, including members of the bivalve genus *Chama*, but for most species such annotations are wanting. It would have been interesting, for example, to know why Kaiser

recognizes two species of the coral-associated muricid genus *Quoyula* (or, perhaps more properly, *Galeropsis*) instead of the single species that most recent authors recognize. The Panamic muricid genus *Pliocopurpura* is represented at Clipperton by the form identified by Kaiser as *P. pansa* (Gould, 1853). The name *P. pansa* refers to the broad-apertured morph of a highly variable species that is usually known by its senior synonym, *P. columellaris* (Lamarck, 1816). The name and the illustration imply that only the broad-apertured form of this species is present at Clipperton, a situation parallel to that of the sister species *P. patula* (Linnaeus, 1758) in the West Indies; and that the narrow-apertured, thick-shelled morph with strong outer-lip teeth, to which the name *P. columellaris* was initially applied, would appear to be absent on Clipperton. Is this so?

An important question about island faunas is whether the species found there maintain viable populations. A virtue of Kaiser's compilation is that dates of collection are given for each species, together with whether specimens were taken dead or alive. Kaiser implies that the two species of the lucinid bivalve genus *Codakia* at Clipperton may no longer be living in the lagoon, as they did when the lagoon was open to the ocean. Many other species are also recorded only as empty shells, implying that many taxa recorded from the atoll are only occasionally present there.

Although it is obvious that a great deal of basic taxonomic work remains to be done, Kaiser's volume offers a solid foundation on which further studies can be built. Questions about island diversity, interactions between species originating in different biogeographic settings, sustainability of island populations, and niche shifts made possible by the absence of major predators and competitors cannot be answered without descriptive faunal accounts of the kind Kaiser has brought together for Clipperton.

Geerat J. Vermeij

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CONTENTS — *Continued*

BOOK REVIEW

The Recent Molluscan Fauna of Île Clipperton (Tropical Eastern Pacific). KIRSTIE L.

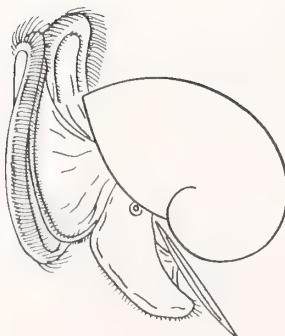
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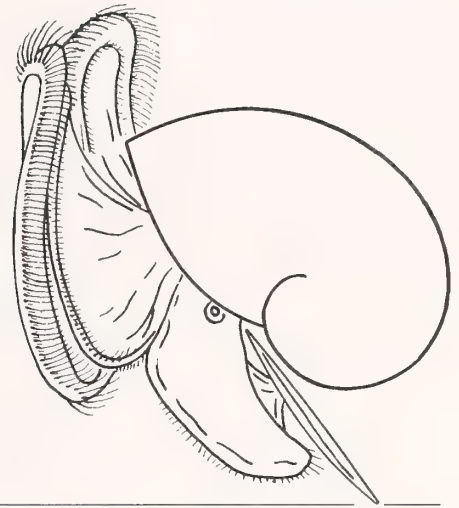
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CONTENTS

- 2L
101
V4X
MOLL
- Synecology of a Springsnail (Caenogastropoda: Hydrobiidae) Assemblage in a Western U.S. Thermal Spring Province
DONALD W. SADA 59
- Two New Species of the Genus *Cerithiopsis* Forbes & Hanley, 1850 (Gastropoda: Cerithiopsidae) from Brazil
RAQUEL MEDEIROS ANDRADE FIGUEIRA AND ALEXANDRE DIAS PIMENTA 72
- A Record of the Invasive Slug *Veronicella cubensis* (Pfeiffer, 1840) in California
R. J. MC DONNELL, A. HANSEN, T. D. PAINE AND M. J. GORMALLY 81
- Developmental Mode in Opisthobranch Molluscs from the Tropical Eastern Pacific Ocean
JEFFREY H. R. GODDARD AND ALICIA HERMOSILLO 83
- Three New Buccinid Species (Gastropoda: Neogastropoda) from Chilean Deep-Water, Including One from a Methane Seep
KOEN FRAUSSEN AND JAVIER SELLANES 97
- Redescription of the Deep-sea Wood Borer *Neoxylophaga teramachii* Taki & Habe, 1950 and its Assignment to the Genus *Xyloredo* (Bivalvia: Myoida: Pholadoidea) with Comments on Fossil Pholadoidae
TAKUMA HAGA AND TOMOKI KASE 107
- A Note on *Strombus coronatus* Defrance, 1827 and *Strombus coronatus* Röding, 1798 (Mollusca: Gastropoda)
MATHIAS HARZHAUSER AND GIJS C. KRONENBERG 120

CONTENTS — Continued

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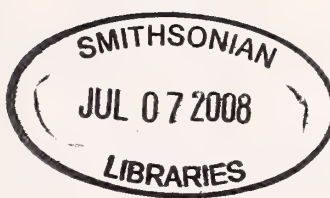
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Synecology of a Springsnail (Caenogastropoda: Hydrobiidae) Assemblage in a Western U.S. Thermal Spring Province

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Abstract. Springsnails are numerically dominant members of benthic communities in many springs of western North America and Australia. Several studies have shown the influence of water chemistry on their abundance and distribution within springs, but little information exists regarding their use of physical aspects of spring environments. Habitat preferences, niche breadth and overlap, and environmental factors influencing the structure of an assemblage of native springsnails (*Pyrgulopsis avernalis*, *P. carinifera*, and *Tryonia clathrata*) and the non-native red-rimmed melania (*Melanoidea turberculata*) gastropod are described in a southern Nevada, USA, thermal spring province. Water temperature, current velocity, and substrate type were the most important physical factors structuring the assemblage. Springbrook wetted width, presence of armored and incised banks, and location of sample sites across the wetted width were also statistically significant, but less important factors. Each species occupied a wide diversity of habitats, but each species also exhibited habitat preferences for a range of depths, velocities, temperatures, or substrates. Niche overlap varied among species and habitats were partitioned among species for a minimum of two environmental resources. Competitive interactions appeared to minimally influence the structure and distributions of species belonging to this assemblage.

Findings suggest that springsnails are restricted to portions of a spring that provide suitable physicochemical conditions, and that each springsnail taxon may exhibit specific habitat requirements. Springsnail extinctions and declines in abundance in western North America and Australia can be attributed to human activities altering the discharge and water depth, substrate composition, current velocity, and water temperature of springs. Novel approaches are required to alter human uses and facilitate restoration, and protect the integrity of these unique arid land aquatic systems.

Key Words: Spring ecology, Hydrobiidae, springsnail ecology, arid land wetlands.

INTRODUCTION

The Hydrobiidae is a worldwide family of primarily freshwater gill-breathing gastropods. Recent taxonomic studies have found an amazing diversity of hydrobiids (commonly referred to as springsnails) in isolated, arid land springs of North America and Australia. More than 120 species in seven genera are known from more than 1000 springs in the western U.S., and 35 species in nine genera from Australia (Ponder et al., 1989; Hershler, 1994, 1998, 2001). Springsnails are restricted to persistent aquatic habitats that are minimally affected by drought (Taylor, 1985) and most species occupy few localized habitats within a limited geographic area (Hershler, 1998). They are usually the most abundant benthic macroinvertebrate in springs where they occur, and springs occupied by more than one springsnail species are uncommon.

In spite of their taxonomic diversity and their abundance in springs, few ecological studies have been conducted. Information is limited to demographic

studies showing the influence of temperature on *Pyrgulopsis brunequensis* demography and feeding in springs along the Snake River of southern Idaho (Mladenka and Minshall, 2001), and relationships between CO₂ concentrations and *P. montezumensis* abundance in northern Arizona (O'Brien and Blinn, 1999). Richards et al. (2001) examined spatial relationships in an assemblage of three snails including *Taylorconcha serpenticola* and Ponder et al. (1989) examined the influence of several environmental factors on activity and survivorship of several species in mound springs of Australia. These species responded to desiccation, salinity, deoxygenated water, water temperature, and submersion but the authors were unable to quantify relationships between habitat zones and springsnail abundance. Qualitative observations during taxonomic and biogeographic surveys suggested that abundance within a spring is influenced by water depth, current velocity, substrate composition, and aquatic vegetation (e.g., Hershler and Sada, 1987; Hershler, 1998). These observations indicate that each

species occupies a unique habitat within a spring, but they have not been supported by quantitative studies examining relationships between spring environment, microhabitat use, and assemblage structure. Ecological information is needed to provide insight into isolating mechanisms that have facilitated development of this diverse fauna in small, isolated habitats. This information is also important in determining how springsnails respond to human activities that alter springs. These small wetlands support much of the aquatic life in arid lands and most springs have been degraded by livestock, diversion, and introduction of non-native species (Sada et al., 1992; Shepherd, 1993; Hubbs, 1995; Myers and Resh, 1999; Sada and Vinyard, 2002; Sada et al., 2005). These activities have justified listing several springsnail species as endangered in the western U.S., and Hershler (1998) and Sada (field notes) recorded three extinctions and extirpation of 13 populations in the past decade.

In this study, an assemblage of four species (three springsnails and one non-native mollusk) was examined in a thermal spring province to: 1—determine physical factors (in addition to temperature) affecting assemblage structure, 2—quantify microhabitat use, and 3—determine if habitat use differs among species. The spring province includes approximately 30 springs that discharge a total of 1.3 m³/sec. Discharge and temperature at individual springs ranges from 10–200 l/min, and 24.5–31.8°C, respectively. This assemblage included *Pyrgulopsis avernalis* and *P. carinifera* that are endemic to this province, and *Tryonia clathrata* that is endemic to thermal springs along the pluvial White River system in eastern Nevada (Hershler, 1994, 2001). All of these species are small. The shell height of *P. avernalis* ranges from 2.4 mm to 4.3 mm, for *P. carinifera* from 3.8 mm to 5.0 mm, and for *T. clathrata* from 2.9 mm to 7.0 mm. The red-rimmed melania (*Melanoides tuberculata*, family Thiaridae), which is native to Asia (Burch and Tottenham, 1980), also inhabits these springs. Shell height of adult melania is from 1 cm to 3 cm. Quantitative studies have not assessed the influence of this species on springsnails. Hershler and Sada (1987) noted that springsnail abundance may be decreased in its presence, and Pointier et al. (1993) and De Marco (1999) found that it detrimentally affected native gastropod abundance.

This work was one component of studies examining the benthic macroinvertebrate communities in this spring province, which will be the subject of a subsequent article.

SITE DESCRIPTION

Studies were conducted in a spring province (collectively referred to as 'Warm Springs') that forms the

Muddy River in Clark County, Nevada (Figure 1). The Muddy River flows approximately 35 km into the Colorado River (which is now within the Overton Arm of Lake Mead). The springs creating the Muddy River are located at approximately 500 m elevation and scattered over approximately 2,000 hectares. Water flows through approximately 4 km of springbrook before forming the Muddy River. Water temperature at spring sources is approximately 32°C, and combined discharge from the province is a relatively constant 1.5 m³/sec (Eakin, 1964). Discharge from individual springs ranges from approximately 0.0028 to 0.17 m³/sec and spring brooks are bordered by ash (*Fraxinus velutina*), mesquite (*Prosopis* sp.), non-native salt cedar (*Tamarix* sp.), and fan palm (*Washingtonia filifera*). These woody species are interspersed with grasses (mostly *Distichlis spicata*) and perennial herbs. Springbrooks support diverse aquatic habitats from low gradient brooks that meander over fine substrates to higher gradient brooks where swift water flows over gravel and cobble substrates. General characteristics of spring brooks that were sampled during this study are summarized in Tables 1 and 2. In addition to mollusks, these springs support a number of rare fishes and other aquatic macroinvertebrates, many of which are endemic to Warm Springs (U.S. Fish and Wildlife Service, 1996; Hershler, 1994, 2001; Schmude, 1999; Polhemus and Polhemus, 2002; Sada and Vinyard, 2002).

Native Americans had settlements near Warm Springs, and in the early 19th Century it was settled by white men. Its springs have been altered for recreation and diversion, channelization, and siltation from agriculture, and non-native fishes and aquatic invertebrates have been introduced (Scoppettone, 1993). These alterations reduced native fish abundance and resulted in listing the Moapa dace (*Moapa coriacea*) as endangered by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 1996). Since the early 1980s, Moapa dace recovery programs have restored six springs and approximately 600 m of spring brook (approximately 15 percent) to natural condition.

METHODS

Data Collection

Aquatic habitat parameters (Tables 1 and 2) and mollusks were sampled in 84, 10 cm × 12 cm quadrats at 21 stations located at predetermined distances from five spring sources (two with long and three with short spring brooks) (Table 3) during the autumn of 1996. Sample stations included the diversity of habitats in first-order spring brooks, and were placed near springs sources and along the downstream continuum to the confluence of the nearest tributary spring brook. The distance of stations from spring sources varied because

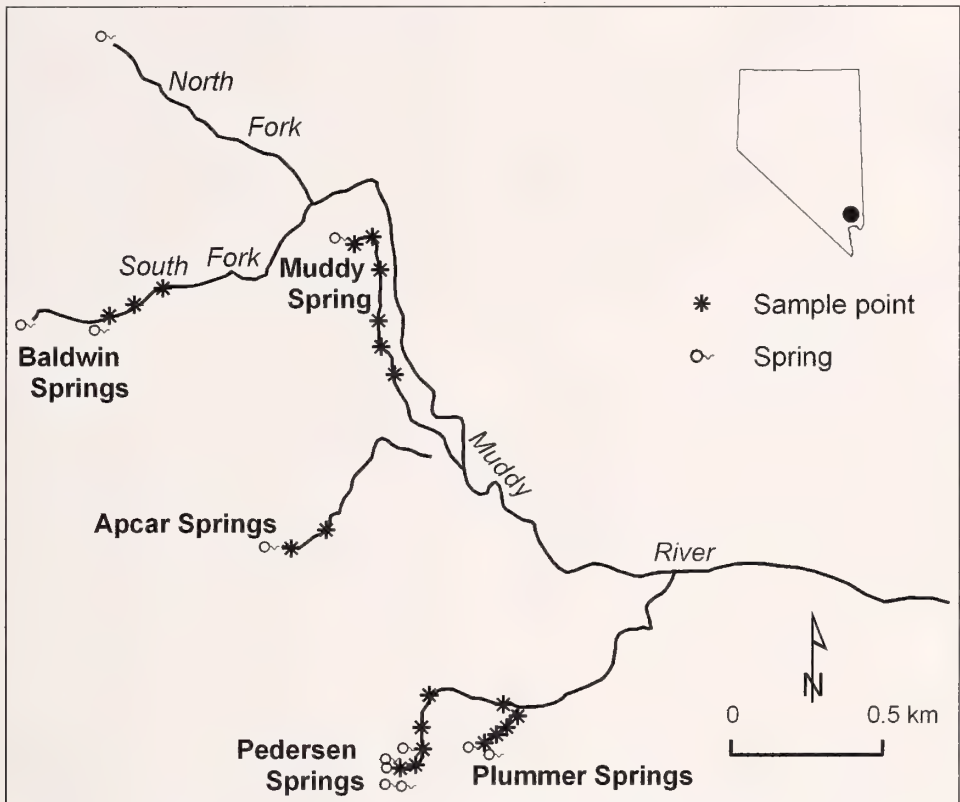


Figure 1. Map showing the approximate location of sample sites (*) and major springs in the ‘Warm Springs’ province that combine to form the Muddy River, Clark County, Nevada.

some reaches were not easily accessed, some spring brooks were less than 50 m long, and longer intervals occurred in large springs with long spring brooks. Each station consisted of four transects spanning the wetted

width (spaced 1 m apart and oriented perpendicular to the thalweg) where mollusk samples and aquatic habitat measurements were collected from two mid-channel and two springbrook margin quadrats. Mid-channel quadrats were placed along first and third

Table 1

Median and range of aquatic habitat parameters measured (units shown in parentheses) within quadrats and at 21 stations where mollusks were sampled in Warm Springs, upper Muddy River. All variables used in CCA to examine relationship between environmental factors and mollusk assemblage structure. * = parameters measured in quadrats, ** = parameters measured along transects, all others measured at stations.

Element	Median	Range
Water Depth (cm)*	16	2–70
Water Velocity (cm/sec)*	20	0–109
Springbrook Width (cm)**	180	40–530
Water Temperature (°C)	31.3	24.5–31.8
Dissolved Oxygen (mg/l)	5.1	4.1–5.7
Electrical Conductance (µmhos/cm)	1100	1050–1100
pH	7.6	7.4–7.6
Riparian Cover (percent)**	90	2–100

Table 2

Proportion of quadrats and spring brook banks where substrate and channel features, respectively, occurred during mollusk sampling in Warm Springs, upper Muddy River, Clark County, Nevada. n = 84 for Substrate Features (all measured in quadrats) and n = 168 for Channel Features (all measured where transects intersected banks). All variables used in CCA.

Substrate Feature	Proportion	Channel Feature	Proportion
Fines	0.28	Stable Channel	0.87
Sand	0.18	Incised Banks	0.75
Gravel	0.44	Bank Overhang	0.57
Cobble	0.11	Bank Perennial	0.42
		Vegetation	
CPOM	0.16	Grassy Banks	0.14
Palm Roots	0.43	Armored Banks	0.14

Table 3

Spring brook names and the approximate distance of sample stations from each spring source.

Springbrook Name	Locations (m)
Pedersen Spring	10, 25, 60, 120, 200, 500
Muddy Spring	10, 25, 60, 120, 180, 280
Plummer Spring	10, 25, 60, 120
Apcar Spring	25, 60
South Fork Muddy River Spring	25, 60, 120

transects, and right and left bank quadrats on transects two and four, respectively (bank quadrats scored 1 and mid-channel scored 0 for canonical correspondence analysis). Channel features (Table 2) and springbrook width were recorded across each transect and bank features were recorded where transects intersected the banks. Water depth and mean water column velocity (measurement taken at 60 percent water depth) were measured at the center of each quadrat, and occurrence of substrate types, filamentous green algae, palm roots, and coarse particulate organic matter (CPOM) were scored as present (1) or absent (0) from a quadrat. Electrical conductance (EC), dissolved oxygen concentration, temperature, and pH were measured at each station (using Model 33 [EC and temperature] and Model 57 YSI [dissolved oxygen] meters, and an Oakton pHTestr 2 handheld meter). A Marsh-McBirney Model 2000 current meter was used to measure current velocity. Although this velocity measurement may weakly quantify benthic microhabitats, correlation between these velocities suggests that conditions at mean water column are indicative of velocities over substrate. pH and dissolved oxygen meters were calibrated daily and other meters calibrated according to manufacturer specifications. Mollusks were collected by roiling substrate within the quadrat for 10 sec to flush material downstream into a 250 micron mesh net that was held in a vertical frame and secured to the quadrat. Samples were preserved in 90 percent ethyl alcohol and returned to the laboratory for identification, and enumeration. Identification was made using descriptions in Hershler (1994, 2001). Samples are archived at the Desert Research Institute, Aquatic Ecology Laboratory, Reno, Nevada.

Data Analysis

Environment-Assemblage Relationships: Relationships between aquatic and channel environments and assemblage structure were examined with canonical correspondence analysis (CCA) using Canoco 4.0 for Windows. CCA axis scores were standardized using methods of Hill (1979), scaled to optimize the representation of species, and Monte Carlo simulation

(1000 iterations) tested the hypothesis that there was no relationship between species and environment matrices. A total of 22 measured and categorical habitat features were included in the analysis (EC and pH did not differ among stations and were not used in the CCA). The CCA is a multivariate direct gradient analysis that analyzes unimodal data to assess species distribution along environmental gradients. It performs multiple linear least-squares regressions with the environment and species abundance as independent and dependent variables, respectively (ter Braak and Prentice, 1988; Jongman et al., 1987; Palmer, 1993).

Microhabitat Use: Habitat preference was calculated for water depth, temperature, and velocity, and the presence of substrate types. With the exception of water depth, CCA showed these variables were most important to structuring the molluscan assemblage (Figure 2, Table 4). Preferences for water depth were calculated because preliminary analysis indicated these species occupied a diversity of available depths. Preference was calculated using the formula of Jacobs (1974): $D = r - p / r + p - 2rp$; where p is the proportion of the resource available in the habitat and r is the proportion of the resource utilized by the species. Resource use was categorized as moderate preference (between 0.25 and 0.5) or strong preference (>0.5), or strongly (<-0.5) or weakly avoided (between -0.25 and -0.5). Neither preference nor avoidance were indicated by values < 0.24 and > -0.24 . Niche breadth was calculated using the equation $B = 1 / \sum P_{ij}^2$, where P_{ij} is the proportion of the resource in each category (Levins, 1968), and niche overlap was calculated using the same variables following the equation from Schoener (1970) with revisions by Litton et al. (1981) so that $S = 100(1 - 1/2 \sum |P_{xi} - P_{yi}|)$ where P_{xi} and P_{yi} are the proportion of resource use in each category for the two species being compared. Niche breadth values may range from 1 to > 14 . Low values are indicative of narrow, limited habitat use and high values indicate wider use of available habitats. Niche overlap values range from 0 to 1 with substantial overlap being indicated by values > 0.5 and differences in use indicated by values < 0.5 . Habitat availability was calculated using records from all quadrats ($n = 84$) and habitat use, and niche breadth and overlap calculations were made by weighting resource utilization in accordance with each species' abundance. Preference, niche breadth, and niche overlap calculations must be interpreted with caution. They are indices that provide insight into relationships in habitat use among species but they are not quantitative descriptions of inter-specific interactions, which can only be determined through experimental manipulation. Similarities among results of these analyses and CCA may guide experimental studies by indicating the relative influence of individual environmental variables on the distribution of species.

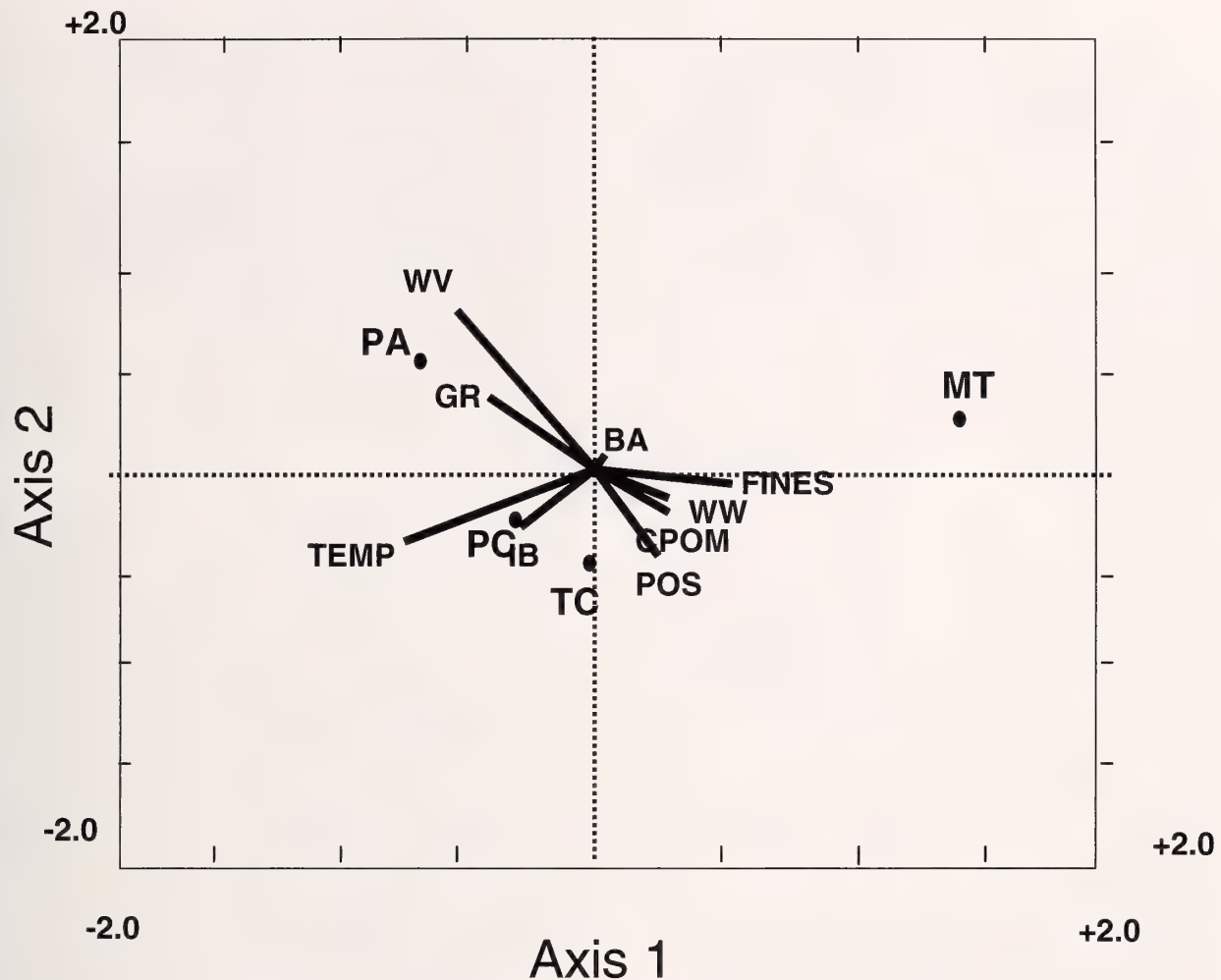


Figure 2. Canonical correspondence analysis biplot showing the relative influence of significant instream and channel environmental parameters on structure of the mollusk assemblage at Warm Springs. The relative influence of each environmental variable is shown by vector length with longer vectors indicating variables with greater importance. PA = *P. averyi*, PC = *P. carinifera*, TC = *T. clathrata*, MT = *M. tuberculata*, WV = mean water column velocity, TEMP = water temperature, GR = gravel, FINES = fines, IB = presence of incised banks, POS = quadrat position, CPOM = coarse particulate organic matter, WW = wetted (spring brook) width, and BA = presence of armored bank.

RESULTS

Environment-Assemblage Relationships: A total of 1282 *P. carinifera*, 704 *P. averyi*, 750 *T. clathrata*, and 283 *M. tuberculata* were collected and tallied. Snail abundance in quadrats ranged from 0 to 346 (equivalent to approximately 29,000/m²), and from 0 to 148 for *P. carinifera*, 0 to 145 for *P. averyi*, 0 to 96 for *T. clathrata*, and 0 to 34 for *M. tuberculata*. Initial CCA revealed nine significant ($P < 0.05$) physicochemical factors were most important to structuring the assemblage (Table 4). Water temperature, mean water column velocity, the presence of some substrates (fines, gravel, CPOM), aspects of channel morphology (incised or armored banks, spring brook width), and

quadrat location (bank vs. mid-channel) were statistically significant variables. Water depth, the presence of roots, algae, other submerged vegetation, sand and cobble substrates, dissolved oxygen concentration, distance from spring source, and bank angle, stability and grassy vegetation had comparatively little influence on assemblage structure. The first axis explained most of the species-environment relationship, all variation was explained by the first three canonical axes, and the total inertia of eigenvalues was 0.814 (Table 5). Monte Carlo simulation (1000 iterations) of species-environment correlations were significant for Axis 1 ($P = 0.001$) and for all canonical axes ($P = 0.001$).

Figure 2 is a CCA biplot where species relationships and environmental factors that were most influential to

Table 4

Inter-set correlations for 22 environmental variables examined during CCA. Variables in bold were statistically significant ($P < 0.05$) and used in final analysis for the biplot in Figure 2. Abbreviations used in Figure 2 shown in parentheses.

Environmental Variable	Axis 1	Axis 2	Axis 3
Water Depth	-0.094	-0.0036	0.0704
Water Velocity (WV)	-0.5619	-0.0036	0.0704
Wetted (Spring Brook) Width (WW)	0.302	-0.0772	0.2246
Presence of Palm Roots	-0.033	-0.01297	-0.0597
Presence of Fines (FINES)	0.5465	0.0196	0.0459
Presence of Sand	-0.1301	0.042	-0.1521
Presence of Gravel (GR)	-0.3831	0.128	-0.041
Presence of Cobble	-0.071	-0.0007	0.1061
CPOM (CPOM)	0.2866	-0.1245	-0.0369
Dissolved Oxygen Concentration	0.0511	0.0855	-0.3521
PH	0.1421	-0.1228	0.1427
Water Temperature (TEMP)	-0.6796	-0.3401	0.0182
Electrical Conductance	-0.0643	-0.1221	0.1527
Bank Angle	0.0965	0.0296	0.1444
Presence of Bank Overhang	-0.1707	0.2148	-0.032
Bank Armor Presence (BA)	0.0965	0.0296	0.1444
Grassy Bank Presence	0.0582	-0.2636	0.188
Presence of Other Perennial Vegetation on Bank	0.0596	-0.234	-0.0447
Incised Bank Presence (IB)	-0.2142	-0.1887	0.0907
Stable Banks	-0.1032	-0.2497	-0.1421
Riparian Cover	-0.0439	0.0816	0.0804
Quadrat Position (Bank or Center) (POS)	0.2823	-0.2859	-0.0651

assemblage structure are illustrated by vector length and the association of each species with each environmental variable. Vector length illustrates that water velocity, temperature, and the presence of fines and

Table 5

Eigenvalues, species-environment correlations, and cumulative percentage variance of species data and species-environment relationship explained by the first three ordination axes of the CCA analysis of the Warm Springs mollusk assemblage.

	Axis I	Axis II	Axis III	Total Inertia
Eigenvalues	0.361	0.123	0.023	0.841
Species-Environment Correlation	0.835	0.748	0.471	
Cumulative Percentage Variance				
Species Data	42.9	57.5	60.3	
Species-Environment Relation	71.2	95.5	100	

gravel were the most influential factors. Quadrat position and the presence of incised banks were moderately influential, and wetted width, and the presence of CPOM and armored banks were least important. The plot indicates these species occupied different habitats. *Pyrgulopsis avernalis* (PA) was associated with higher current velocities (WV), gravel substrate (GR), and higher water temperature (TEMP), and *P. carinifera* (PC) with moderate current velocities and incised (IB), unarmored banks. *Tryonia clathrata* (TC) was associated with moderate temperatures, slower currents, bank quadrats, CPOM, and the absence of gravel and fine substrates. *Melanoides tuberculata* was associated with fine substrate (FINES), wider brooks (WW), cooler temperatures, and lower current velocities.

Microhabitat Use and Resource Partitioning: Habitat preference calculations confirm CCA results and indicate these species partition habitat by temperature, water velocity, and substrate. Niche breadth and overlap values suggested that there were differences in diversity of habitat used by each species and that there was common use of some habitats. *Pyrgulopsis avernalis* occupied a wide diversity of depths ($B = 5.21$), but preferred depths from 30 cm to 40 cm (Figure 3A). It avoided shallow (<15 cm) and deeper water (>45 cm). Niche breadth values indicated that it also occupied a wide variety of current velocities ($B = 7.69$), but it preferred mean water column velocities > 50 cm/sec and strongly preferred velocities approximately 70–110 cm/sec (Figure 4A). It avoided currents < 40 cm/sec and it was most common in mid-channel quadrats where currents were swift and smaller substrates scarce (Table 6). It also preferred gravel, avoided cobbles, and strongly avoided fines, sand, and CPOM (Figure 5A). It occupied the warmest water temperatures in the spring province, preferred temperatures near 32°C ($B = 1.49$), and avoided cooler water (Figure 6A).

Pyrgulopsis carinifera also occupied a diversity of depths ($B = 5.29$), but it preferred habitats < 10 cm deep and avoided depths > 30 cm (Figure 3B). It occupied slow and fast currents ($B = 5.66$) but preferred mean water column velocities from 30 to 40 cm/sec (Figure 4B). Like *P. avernalis*, it occurred in mid-channel quadrats (Table 6), preferred gravel, avoided sand and CPOM, and strongly avoided fines and cobbles (Figure 5B). It also strongly preferred temperatures near 32°C ($B = 1.31$) and avoided cooler water (Figure 6B).

Tryonia clathrata also preferred the warmest waters (Figure 6C), but occupied substantially different microhabitats than either species of *Pyrgulopsis*. *Tryonia clathrata* was most common along spring brook banks where it preferred shallow (<5 cm deep), slow moving

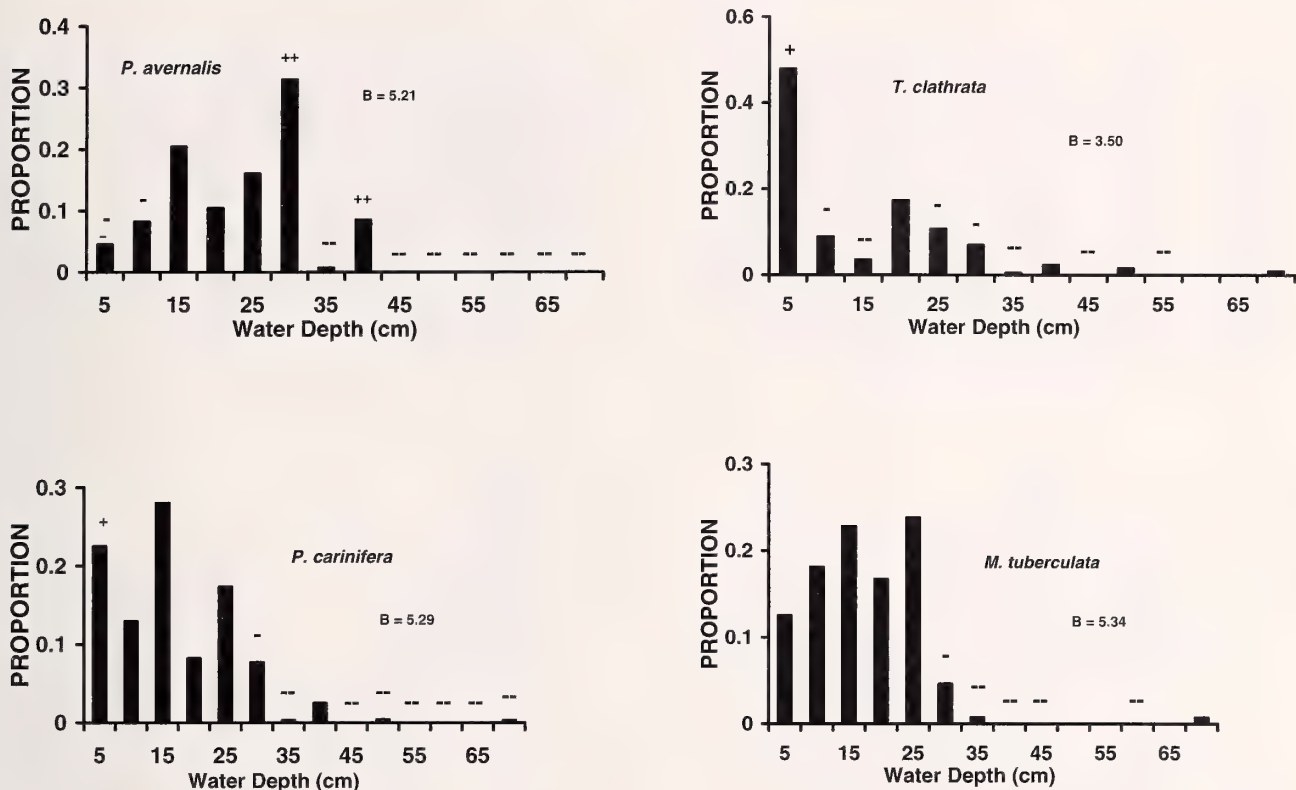


Figure 3. The depth of water occupied by *P. avarnalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. + and ++ = moderately preferred resource categories, respectively, - and -- = moderately and strongly avoided resource categories, respectively. B = niche breadth.

(<20 cm/sec) water while avoiding deeper, swiftly flowing waters (Figures 3C and 4C, Table 6). Small niche breadth values for depth and velocity ($B = 3.50$ and 2.82 , respectively) indicate its comparatively restricted use of shallow depths and slow currents. It strongly preferred sand, preferred fines and CPOM, and strongly avoided gravel and cobbles (Figure 5C).

Melanoides tuberculata occupied a wider diversity of water temperatures than the springsnails ($B = 2.85$), and it strongly preferred temperatures near 25°C and strongly avoided the warm temperatures preferred by springsnails (Figure 6D). Differences between springsnail and *M. tuberculata* preferences for temperature probably account for the importance of temperature in structuring the assemblage that was shown by CCA (Figure 2). It exhibited no preference for water depth but it strongly avoided habitats deeper than 30 cm (Figure 3C). It was most common along springbrook banks (Table 6). Current velocities from 0–10 cm/sec were preferred and mean water column velocities < 10 cm/sec were strongly preferred (Figure 4D). It showed no preference or avoidance of CPOM.

Melanoides tuberculata used habitats similar to those occupied by *T. clathrata* and quite different from both *Pyrgulopsis*-species. Although habitats used by *T.*

clathrata and *M. tuberculata* were similar, *M. tuberculata* strongly preferred the presence of fine substrate and strongly avoided sand, gravel, and cobble (Figure 5D). These two species also appeared to occupy habitats with different temperatures and current velocities (Figures 3D and 4D, respectively). *Tryonia clathrata* occupied shallow habitats (Figure 2D) where sand substrate was associated with slightly swifter current while *M. tuberculata* occupied habitats where fine substrates were associated with very low current velocities. These characteristics suggest that *M. tuberculata* may be relatively tolerant of nocturnal decreases in dissolved oxygen concentrations that can be associated with fine substrates. Use of this habitat type is consistent with observations of its habitat use by Dudgeon (1989), Gutiérrez et al. (1997), and Duggan (2002). Differences in habitat use by springsnails and *M. tuberculata* suggest that their interactions may be minimal at Warm Springs.

Niche overlap values generally confirm habitat use shown in Figures 3–5. Values were < 0.5 between *T. clathrata* and both species of *Pyrgulopsis* for water depth and substrate type (with exception of 0.638 between *T. clathrata* and *P. carinifera* for depth), which suggests that intra-generic habitat use of species in this

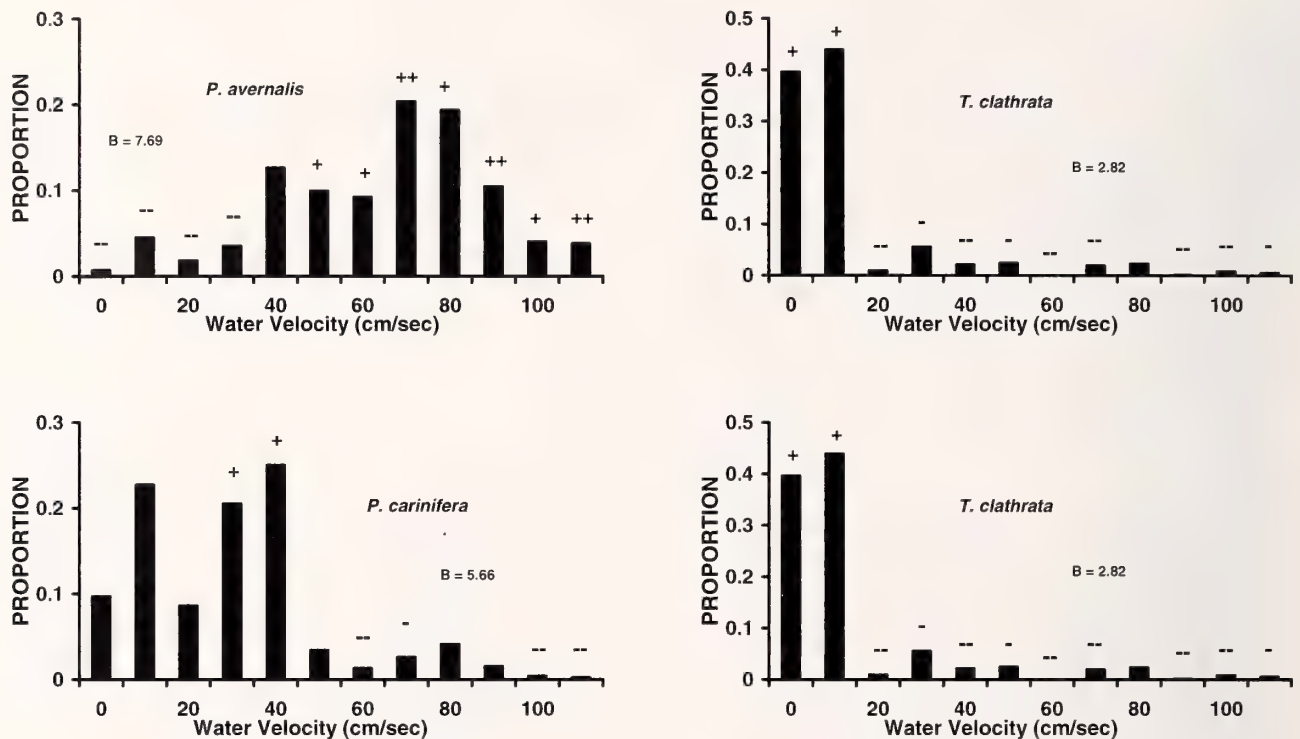


Figure 4. Mean water column velocity of habitats occupied *P. aernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. Preference and avoidance illustrated as in Figure 3.

springsnail assemblage is minimal (Tables 7 and 8). Niche overlap values for *P. aernalis* and *P. clathrata* were low for current velocity (<0.35) and > 0.5 for water depth and substrate type, which indicates that habitat use by these species is similar and differs primarily in the use of fast and moderate currents by *P. aernalis* and *P. clathrata*, respectively. Overlap between the springsnail assemblage and *M. tuberculata* was high for water depth, but overlap was also high between velocities used by the melania, *P. carinifera*, and *T. clathrata* (Table 7). Highest overlap in current velocity occurred between *T. clathrata* and *M. tuberculata*, and lowest was between *P. aernalis* and *M. tuberculata* (Table 7). Overlap for fines, gravel, and cobble substrate use was relatively high among all species in the assemblage, but overlap was low between both *Pyrgulopsis* species and *T. clathrata* for use of sand (Table 8). Overlap for use of sand was also low between *M. tuberculata* and *T. clathrata* (Table 8), which confirms results of calculations showing *M. tuberculata* and *T. clathrata* preferred fines and sand, respectively.

DISCUSSION

Springsnails represent the most diverse family of gastropods in western North America and many species occupy the smallest aquatic habitats in the

most arid regions of the continent. In these areas, most populations inhabit isolated springs and spring provinces on valley floors and along the base of mountain blocks. Populations rarely inhabit springs higher than 2,400 m elevation. Temperature and EC of springsnail habitats range from 10°C to 40°C and from 70 $\mu\text{mhos/cm}$ to 37,000 $\mu\text{mhos/cm}$, respectively (Hershler and Sada, 1987; Sada and Deacon, 1995; Hershler, 1998). The amount of habitat occupied by springsnail populations ranges from $< 1 \text{ m}^2$ in small springs to $> 100 \text{ m}^2$ in large springs. Hershler (1998) estimated that the density of some populations may reach 10,000/ m^2 . Most populations are relictual in aquatic systems that have persisted since ancient pluvial periods, and they are restricted to springs with minimal environmental

Table 6

Proportion of individuals of each species of mollusk occurring in spring brook mid-channel and bank quadrats sampled at Warm Springs.

Species	Mid-Channel	Bank
<i>P. aernalis</i>	0.80	0.20
<i>P. carinifera</i>	0.53	0.47
<i>T. clathrata</i>	0.18	0.82
<i>M. tuberculata</i>	0.24	0.76

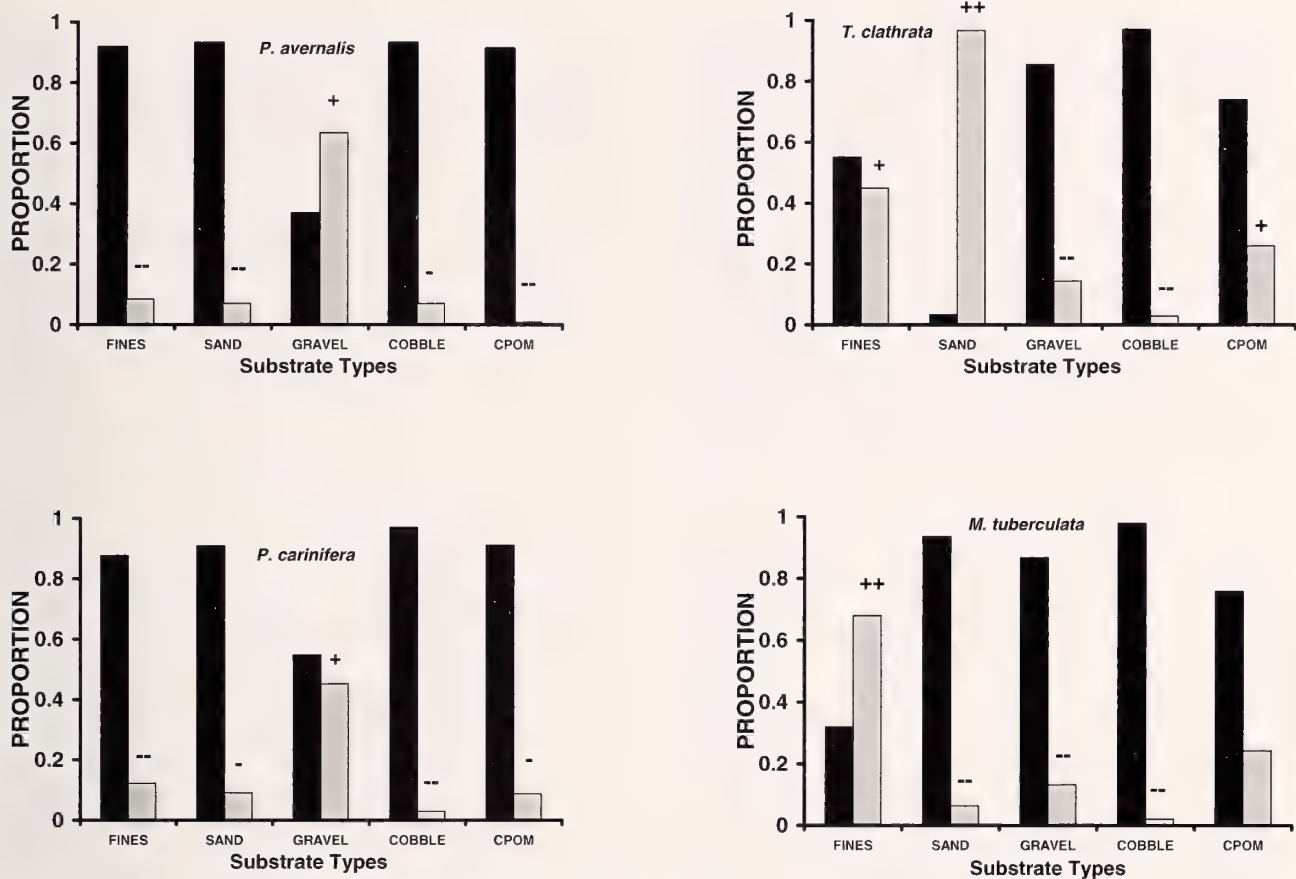


Figure 5. The proportion of *P. aernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata* that were associated with the presence (□) and absence (■) of different substrates. Preference and avoidance shown only for occupation of quadrats with the presence of a substrate type listed. Preference and avoidance illustrated as in Figure 3.

variability (Taylor, 1985). As with other crenobiontic species, densities are greatest near spring sources where physicochemical environments are relatively stable compared to downstream reaches of spring brooks where seasonal and daily environmental variability is relatively high and springsnails are sparse or absent (Noel, 1954; Hershler, 1998; McCabe, 1998). They do not inhabit reaches that dry on a regular basis, but they may colonize downstream reaches where stressful events such as flooding and drying are infrequent.

Past quantitative studies suggest that springsnails preferentially occupy limited portions of springs with suitable chemistry. In laboratory experiments O'Brien and Blinn (1999) demonstrated that *P. montezumensis* inhabited a limited reach of spring brook where CO₂ concentrations ranged from 110–315 mg/L. They did not occupy upstream reaches where concentrations were greater and downstream reaches where concentrations were less. Annual patterns of variability in *P. bruneauensis* density and its preference for upstream portions of spring brook were attributed to water temperature by Mladenka and Minshall (2001). In

experiments with springsnail assemblages in mound springs of Australia, Ponder et al. (1989) demonstrated the influence of several environmental factors on activity levels and survivorship of one amphibious species and several aquatic species. Each of these species exhibited intolerance to desiccation, low and elevated salinity concentrations, deoxygenated water, low and elevated water temperature, and to varying exposure to submersion. Behavioral responses to light also varied among species. These studies also recorded the relative abundance of several species in eight zones (e.g., spring source, upper part of outflow, middle part of outflow, etc.) in a number of springs. Patterns of zonal occupation were weak, but each assemblage typically included one amphibious species and one large species, and from one to three small aquatic species. They also concluded that springsnail niche potential was fully exploited in these springs and that introduction of species from other springs was therefore unlikely.

The study at Warm Springs showed that structure of this assemblage of native and non-native mollusks was influenced by water temperature and several physical

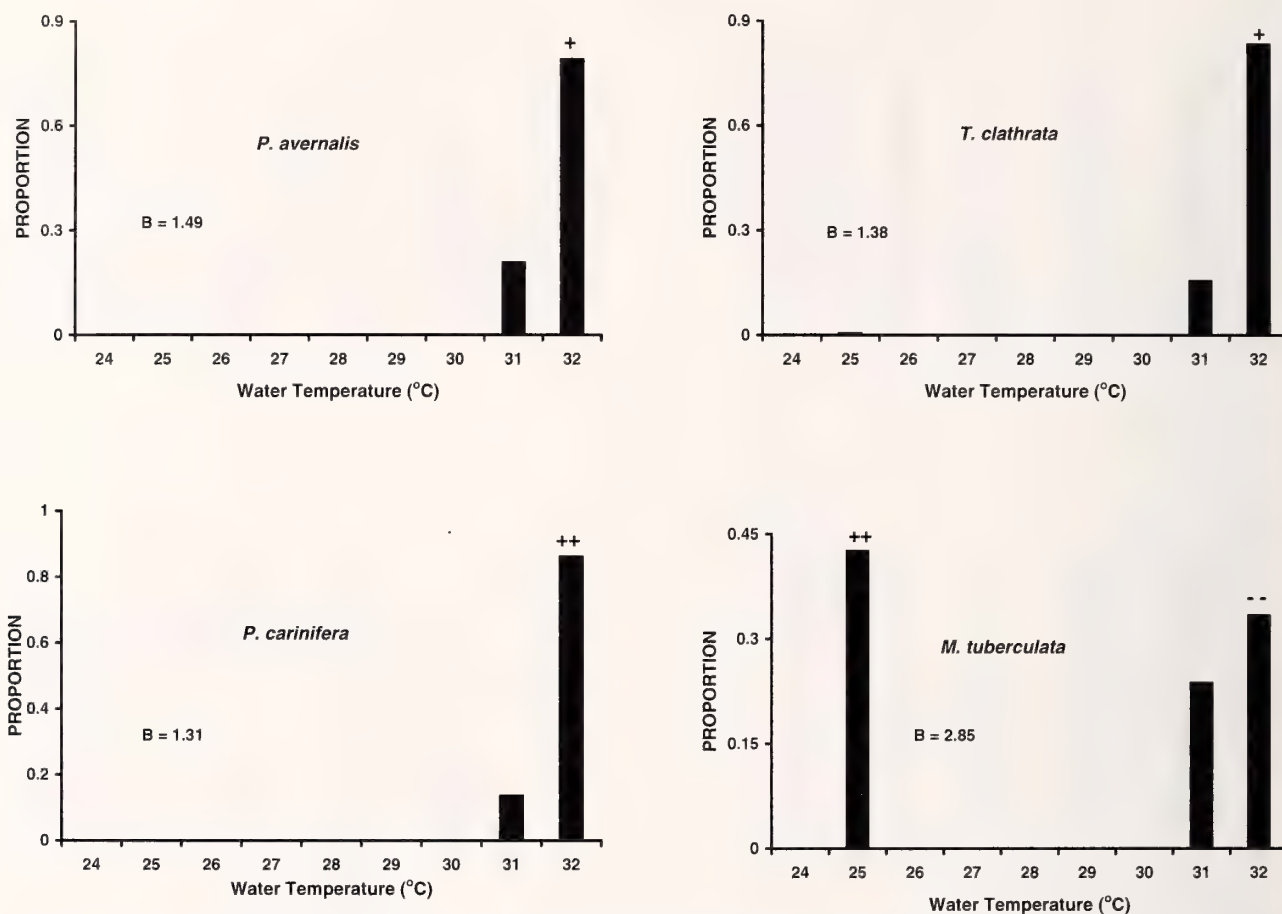


Figure 6. Water temperature of habitats occupied by *P. avernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. Preference and avoidance illustrated as in Figure 3.

elements of the aquatic and spring brook bank environment. These conclusions appear to confirm qualitative observations made during taxonomic studies. They are also consistent with observations by Mladenka and Minshall (2001) that water temperature was an important element of their occupied habitat. Although springsnails at Warm Springs preferred warm water, preferences for temperature did not differ among these species and temperature was not an important factor segregating springsnail habitat use.

Springsnails at Warm Springs occupied a wide diversity of aquatic habitats, which was indicated by relatively high niche breadth values for each species in several habitat elements. Depths, velocities, and substrates occupied by *T. clathrata* were generally more specific than those occupied by either species of *Pyrgulopsis*. Both *Pyrgulopsis* generally occupied deeper and swifter water, and larger substrates than *T. clathrata*, which preferred water < 5 cm deep, velocities < 20 cm/sec, and sand and fine substrates.

Additional partitioning among assemblage members is suggested by the use of mid-channel and springbrook

margin habitats. Although each species occurred across springbrooks, most *T. clathrata* occurred along spring brook margins, *P. carinifera* was relatively evenly distributed between margins and the mid-channel, and *P. avernalis* was most abundant in mid-channel habitats. This appears to be consistent with habitat

Table 7

Niche overlap values for water depth and mean water column velocity among mollusks in Warm Springs, Clark County, Nevada. Abbreviations for species as shown in Figure 2.

	Water Depth			
	PA	PC	TC	MT
PA		.678	.469	.649
PC	.366		.638	.789
TC	.197	.482		.579
MT	.159	.502	.877	
Mean Water Column Velocity				

Table 8

Niche overlap values for fines, sand, gravel, and cobble substrates among mollusks in Warm Springs, Clark County, Nevada. Abbreviations for species as shown in Figure 2.

	Fines/Sand			
	PA	PC	TC	MT
PA		.961/.979	.635/.103	.404/.994
PC	.818/1		.674/.124	.443/.973
TC	.510/1	.692/1		.769/.097
MT	.500/.991	.500/.991	.500/.991	
	Gravel/Cobble			

preferences exhibited by each species. *Tryonia clathrata* occupied shallow, slow habitats and fine substrates that occurred along springbrook banks. *Pyrgulopsis avernalis* was most abundant in mid-channel habitats where substrates are larger and depths and current velocities greatest and *Pyrgulopsis carinifera* preferred slower water and moderate depths that are lateral habitats in mid-channel and along springbrook margins. Preferential occupation of margin and mid-channel habitats suggests that these springsnails may exhibit zonal preferences of habitat use. Differences between this observation and conclusions by Ponder et al. (1989) that zonal preferences were not apparent may be attributed to sample techniques. The wide range in springsnail density within 120 cm² quadrats (range from 0 to 346 springsnails) at Warm Springs suggests there is wide spatial variability in springsnail abundance in a spring and that sample methods using large quadrats may yield weak relationships between springsnail abundance and characteristics of the spring environment. Determining these relationships appears to require quantitative sampling within a small area. Sampling springsnail abundance and habitat characteristics within 120 cm² quadrats appears suitable to examination these relationships.

Observations at Warm Springs provide insight into the potential effects of the *M. tuberculata* on springsnail populations. Observations of potential competitive interactions between *M. tuberculata* and several species of *Tryonia* and *Pyrgulopsis* in Ash Meadows, another thermal spring province in southern Nevada, that were hypothesized by Hershler and Sada (1987) were not confirmed at Warm Springs. Niche overlap between *M. tuberculata* and both species of Warm Springs *Pyrgulopsis* was small for all measured habitat elements. Overlap between *M. tuberculata* and *T. clathrata* was more extensive with both species occupying marginal, slow moving habitats with small substrate. In spite of these similarities, interactions appeared to be minor because they utilized different temperatures, substrates, and water velocities. *Melanoides tuberculata* preferred

cooler water, finer substrate, and slower currents than *T. clathrata*. Differences in habitat use among springsnails and *M. tuberculata* suggest that competitive interactions between these mollusks are relatively minor and that presence of the *M. tuberculata* minimally influences the abundance or habitat use of springsnails at Warm Springs.

Physiological requirements of springsnails demonstrated by Ponder et al. (1989), O'Brian and Blinn (1999), and Mlandeka and Minshall (2001) and springsnail preference for physical components of the environment at Warm Springs suggest that each taxon may be restricted to portions of a spring that provide suitable physicochemical conditions. Additionally, it suggests that springsnail abundance and distribution may be a function of factors that alter these conditions. These observations have wide implications for springsnail biogeography and conservation by suggesting that each taxon may be adapted to comparatively specific physicochemical aspects of their 'home' springs. These rather specific adaptations may be important factors limiting springsnail dispersal and restricting most taxa to springs with similar environments within a limited geographic area. Several recent articles have noted the vulnerability of springsnails to extirpation because of their limited distribution and life history requirements (e.g., Hershler, 1998; Hurt and Hedrick, 2004). Studies at Warm Springs provide quantitative evidence that springsnail abundance may be affected by any factor affecting water temperature (e.g., springbrook diversion, integrity of riparian vegetation), and the quality and heterogeneity of spring habitats. Human activities that reduce environmental heterogeneity (e.g., reduce discharge, channelize, or alter springbrook bank morphology and vegetation) are likely to reduce springsnail abundance or extirpate populations because they alter elements of the environment that define springsnail habitat. Effects of reduced habitat quality and heterogeneity by channelization, siltation, and diversion on springsnail abundance are apparent at Warm Springs where springsnails are scarce or absent from approximately 85 percent of historically occupied springbrooks. In spite of these declines, these springsnail populations appear to be comparatively resilient because their abundance rapidly increased following springbrook restoration for Moapa dace. Reestablishing springsnails in their historic range will require restoring springbrook characteristics and minimizing factors that reduce environmental heterogeneity, such as decreased discharge attributed to diversion and groundwater use.

Over the past decade, Scoppettone (1993) and Scoppettone et al. (1992) delineated characteristics of Moapa dace habitat use, and showed that adults are most common in deep, comparatively large habitats where they can hold near mid-water column and feed

on drifting macroinvertebrates. This information has been integrated into conservation programs to enhance and protect Moapa dace from non-native fishes and activities that have adversely modified springbrooks and the Muddy River. Springsnail preference for relatively shallow habitats with diverse substrate composition suggests that springbrook restoration designed solely for Moapa dace may not provide sufficient heterogeneity for springsnails.

The declining status of springsnails and their sensitivity to habitat alteration is an indicator of the ecological consequences of activities that degrade springs. This suggests that changes in management are necessary to maintain biotic integrity and prevent future declines in crenobiotic species and habitats that support a large portion of the aquatic biodiversity in arid lands.

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Two New Species of the Genus *Cerithiopsis* Forbes & Hanley, 1850 (Gastropoda: Cerithiopsidae) from Brazil

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Abstract. This paper presents a review of the taxonomy of the species belonging to the genus *Cerithiopsis* Forbes & Hanley, 1850 from Brazil, that are characterized by the two adapical rows of nodules in each teleoconch whorl fused together on the initial teleoconch whorls, then becoming gradually separated on the subsequent ones. The following species are reported for the first time from Brazilian coast: *C. fusiformis* (C. B. Adams, 1850), originally described from Jamaica; and *C. aimen* Rolán & Espinosa, 1995 and *C. prieguei* Rolán & Espinosa, 1995, both originally from Cuba. Two new species are described: *Cerithiopsis balaustium* and *Cerithiopsis capixaba*, both from the northeast-southeast coast of Brazil. The five species have minor differences in shell shape and sculpture pattern, being easily distinguished by the protoconch sculpture: in *C. fusiformis* it is smooth, with a thin spiral keel in the middle on two abapical whorls; *C. aimen* has a similar smooth protoconch, but lacking any spiral keel; *C. prieguei* bears two thin spiral cords on adapical whorls, connected by thin axial riblets, also, the sutural area of the protoconch is microscopically granulated; *C. balaustium* has a small protoconch with small axial riblets that do not touch the suture; *C. capixaba* has an elongate protoconch with initial whorls finely granulated and subsequent ones with axial riblets that connect the suture.

Key Words: Cerithiopsidae, *Cerithiopsis*, Brazil, South America, taxonomy.

INTRODUCTION

The genus *Cerithiopsis* Forbes & Hanley, 1850 contains marine microgastropods belonging to the family Cerithiopsidae H. & A. Adams, 1853. Along with the family Triphoridae Gray, 1847, Cerithiopsidae composes the largest part of the superfamily Triphoroidea Gray, 1847 (Ponder & Warén, 1988; Ponder, 1998).

The characteristics used in the taxonomy and identification of species of *Cerithiopsis*, particularly the sculpture pattern, are not easily observed, and worn shells or shells lacking the protoconch are often impossible to identify (Laseron, 1951; Marshall, 1978).

There is no consensus concerning the supraspecific classification of *Cerithiopsis*. Some authors (e.g., Jay & Drivas, 2002, following Marshall, 1978) restricted the concept of the genus, adopting other generic names, such as *Joculator* Hedley, 1909, *Horologica* Laseron, 1956, *Mendax* Finlay, 1927 and *Prolixodens* Marshall, 1978; Odé (1989) also considered *Joculator*, but at the subgeneric level. Herein, we adopted *Cerithiopsis* in a broad sense, following Rolán & Espinosa (1995) and Rolán et al. (2007). We avoided the use of other generic names, because we did not have access to soft parts or

radulae, the analysis of which seems to be essential for proper supraspecific classification in this group. Rolán & Espinosa (1995) and Rolán et al. (2007) distinguished, for working purposes, “groups of species” based on color patterns (e.g., brown colour species, banded and variable colored species).

Whereas most species of this genus have three rows of nodules, equidistant or almost equidistant along the entire teleoconch, some species have the two adapical rows of nodules fused together on the first whorls and becoming gradually separated on the subsequent ones, as described for *Cerithiopsis fusiformis* (C. B. Adams, 1850), a widely distributed species in the western Atlantic. During studies on the taxonomy of Brazilian Cerithiopsidae, we found some shells that exhibit such characteristics of teleoconch sculpture, but can be distinguished by other traits. This paper presents the description of two new species from Brazil, as well as the first, local occurrence of three other species that were originally described from the Caribbean region.

MATERIAL AND METHODS

The material used for this paper was collected in several localities along the Brazilian coastline, and is listed

separately for each species, with the number of shells in brackets. The study was based entirely on conchological analyses. The terminology and characters used to identify the species were based on Laseron (1951, 1956), Marshall (1978), Rolán & Espinosa (1995) and Jay & Drivas (2002).

Abbreviations used: MCZ: Museum of Comparative Zoology, Cambridge; MNCN: Museo Nacional de Ciencias Naturales, Madrid; IBUFRJ: Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MNHN: Muséum National d'Histoire Naturelle, Paris; MNRJ: Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro; MORG: Museu Oceanográfico "Eliézer de Carvalho Rios" da Fundação Oceanográfica do Rio Grande, Rio Grande; MZSP: Museu de Zoologia da Universidade de São Paulo, São Paulo; REVIZEE: Recursos Vivos da Zona Econômica Exclusiva; sta: collection station number; NOAN: Navio Oceanográfico "Antares;" NOWB: Navio Oceanográfico "Professor Wladimir Besnard."

SYSTEMATICS

Family Cerithiopsidae H. & A. Adams, 1853

Subfamily Cerithiopsinae H. & A. Adams, 1853

Genus *Cerithiopsis* Forbes & Hanley, 1850

Cerithiopsis Forbes & Hanley, 1850. Type-species by original designation: *Cerithium tubercularis* Montagu, 1803; Recent, Europe.

Diagnosis: Shell of various shapes (conic to ellipsoidal), protoconchs smooth or sculptured with axial and/or spiral ridges, or finely granulated; teleoconch whorls sculptured by usually three spiral cords, crossed by axial ribs, forming small nodules, with various degrees of conspicuousness. Aperture subquadrangular to circular; siphonal canal short and oblique.

Cerithiopsis fusiformis (C. B. Adams, 1850)

(Figures 1–5)

Cerithium fusiforme C. B. Adams, 1850:120–121; Clench & Turner (1950:285, pl. 38, fig. 4).

Cerithiopsis fusiforme: Usticke (1959:42, not illustrated); Jong & Coomans (1988:46, not illustrated); Rolán & Espinosa (1995:132, figs. 2–6, 47).

Cerithiopsis (Cerithiopsis) fusiformis: Vokes & Vokes (1983:18, pl. 27, fig. 6).

Joculator fusiformis: Redfern (2001:74, pl. figs. 310A–B).

Types: Holotype: MCZ 186127, Caribbean Sea, Jamaica; C.B. Adams coll.

Material examined: The holotype and: –Pernambuco: MNHN, [2] Enseada dos Corais, 1984–1989, P. Maestrati col.; –Bahia: IBUFRJ 12906, [2] Baía de Todos os Santos, sta 56vv, 12/iv/1997; IBUFRJ 12907, [1] Baía de Todos os Santos, sta 11vv, 22/iv/1997; IBUFRJ 12908, [18] Baía de Todos os Santos, sta 54vv, 29/v/1997; IBUFRJ 12909, [9] Baía de Todos os Santos, sta 55vv, 03/iv/1997; IBUFRJ 13887, [1] Baía de Todos os Santos, 5/iv/1997; MORG 48812, [3] R. Areia, Abrolhos, i/1985, Eq. MORG coll.; MORG 48811, [1] I. Guarita, Abrolhos, ii/1987, A. Silveira and L. Laurino coll.; –Espírito Santo: IBUFRJ 12905, [1] REVIZEE sta c65 (18°53'37"S, 39°06'23"W, 50 m), 25/iv/1996, NOAN coll.; IBUFRJ 9515, [1] REVIZEE V sta c64 (19°17'42"S, 38°02'06"W, 63 m), 25/iv/1996, NOAN coll.; IBUFRJ 12903, [12] REVIZEE sta vv38 (19°44'S, 38°24'W, 71.4 m), 29/ii/1996, NOAN coll.; MNRJ 11887, [3] REVIZEE sta vv38 (19°44'S, 38°24'W, 71.4 m), 29/ii/1996, NOAN coll.; MORG 48816, [39] Aracruz, 1/viii/1988, Vera Abud coll.; IBUFRJ 12904, [6] REVIZEE sta c62 (20°30'02"S, 37°28'51"W, 96 m), 25/iv/1996, NOAN coll.; IBUFRJ 10049, [1] REVIZEE V sta c61 (20°30'38"S, 37°19'06"W, 88 m), 24/iv/1996, NOAN coll.; IBUFRJ 12900, [1] REVIZEE sta vv21 (20°38'S, 40°00'W, 33 m), 26/ii/1996, NOAN coll.; –Rio de Janeiro: IBUFRJ 13665, [3] Praia da Figueira, Angra dos Reis, 1998, C. Alvarenga coll.; MORG 41970, [1] off Macaé, sta 3207, 12/iv/1997, Oceanographic Vessel "Victor Hensen" coll.

Cerithiopsis aimen Rolán & Espinosa, 1995

(Figures 6–11)

Cerithiopsis aimen Rolán & Espinosa, 1995:142, figs. 27–30; Boyko & Cordeiro (2001:27).

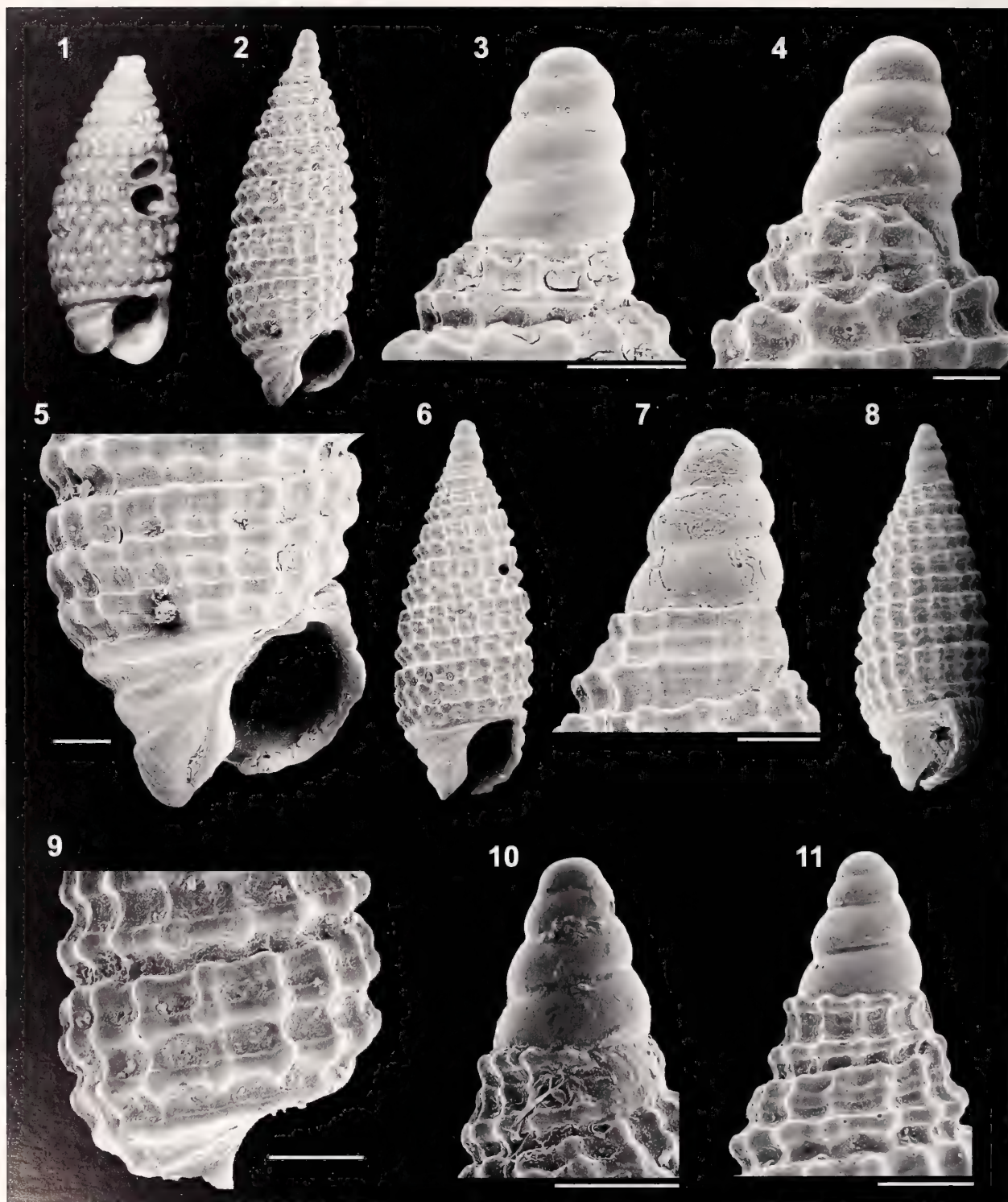
Types: Holotype: MNCN 15.05/17220, Cienfuegos Bay, Cuba; one paratype at AMNH 226504.

Material examined: The holotype and: IBUFRJ 12902, [2] REVIZEE sta vv31 (18°52'S, 39°35'W, 22.8 m), 28/ii/1996, NOAN coll.; MNRJ 11889, [1] REVIZEE sta vv31 (18°52'S, 39°35'W, 22.8 m), 28/ii/1996, NOAN coll.; IBUFRJ 15373, [1] REVIZEE VI sta y7 (77 m); IBUFRJ 15565, [1] Baía de Todos os Santos, Bahia state, 5/iv/1997; IBUFRJ 15564, [4] Baía de Todos os Santos, Bahia state sta 11vv, 22/iv/1997.

Cerithiopsis prieguei Rolán & Espinosa, 1995

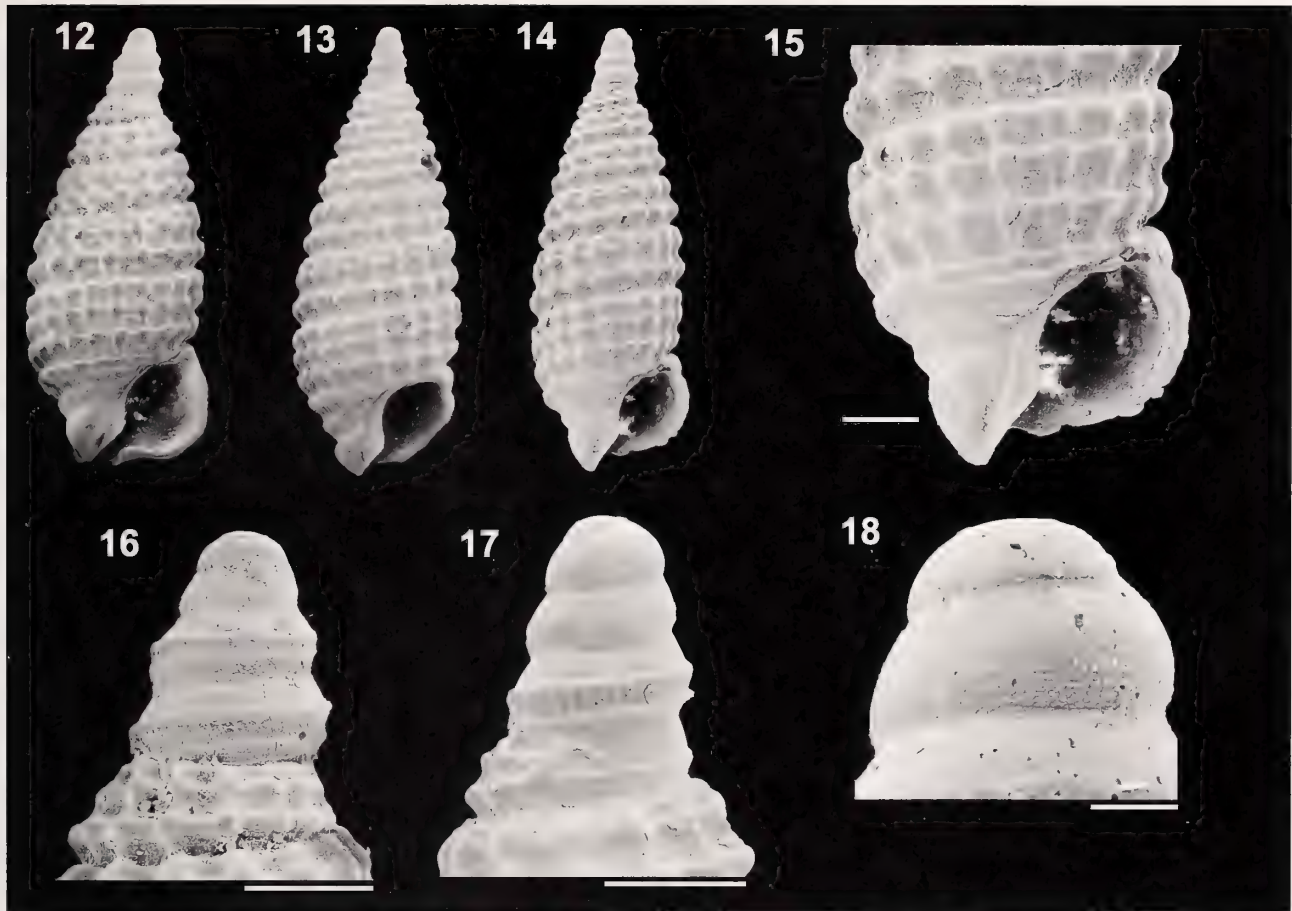
(Figures 12–18)

Cerithiopsis prieguei Rolán & Espinosa, 1995:142, figs. 31–34, 45; Boyko & Cordeiro (2001:28).



Figures 1–5. *Cerithiopsis fusiformis*. 1. holotype (MCZ 186127); 2–3, 5. IBUFRJ 12906; 4. IBUFRJ 12907; 1–2. whole shells (lengths: 3.0 mm); 3–4. protoconchs; 5. last whorl. Scale bars: 200 μ m.

Figures 6–11. *Cerithiopsis aimen*. 6–7. holotype (MNCN 15.05/17220); 8–11. IBUFRJ 12907; 6, 8. whole shells (respective lengths: 3.2 mm, 2.1 mm); 7, 10–11. protoconchs; 9. last whorl. Scale bars: 200 μ m.



Figures 12–18. *Cerithiopsis prieguei*. 12, 16. holotype (MNCN 15.05/17221); 13–15, 17–18. IBUFRJ 14139; 12–14. whole shells (respective lengths: 2.2 mm, 2.5 mm, 2.0 mm); 15. last whorl; 16–17. protoconchs; 18. detail of early protoconch whorls. Scale bars: 15–17: 200 µm; 18: 50 µm.

Types: Holotype: MNCN 15.05/17221, La Habana, Cuba; several paratypes listed in Rolán & Espinosa (1995).

Material examined: The holotype and: IBUFRJ 14139, [3] REVIZEE sta vv38 (19°44'S, 38°22'W, 71.4 m), off Espírito Santo state, 29/ii/1996, NOAN col.; MNRJ 11888, [3] REVIZEE sta vv38 (19°44'S, 38°22'W, 71.4 m), off Espírito Santo state, 29/ii/1996, NOAN col.

Cerithiopsis balaustium n.sp.

(Figures 19–23)

Type material: holotype: MZSP 86307 REVIZEE sta 6666 (24°17.129'S, 44°12.149'W, 163 m), off São Paulo state; paratypes: IBUFRJ 15223, [1] Baía de Todos os Santos, Bahia state sta 11vv, 22/iv/1997; IBUFRJ 15566, [1] Baía de Todos os Santos, Bahia state, sta 54vv, 29/v/1997; IBUFRJ 15371, [1] REVIZEE VI sta y7 (77 m); MZSP 86306 [3] REVIZEE sta 6666

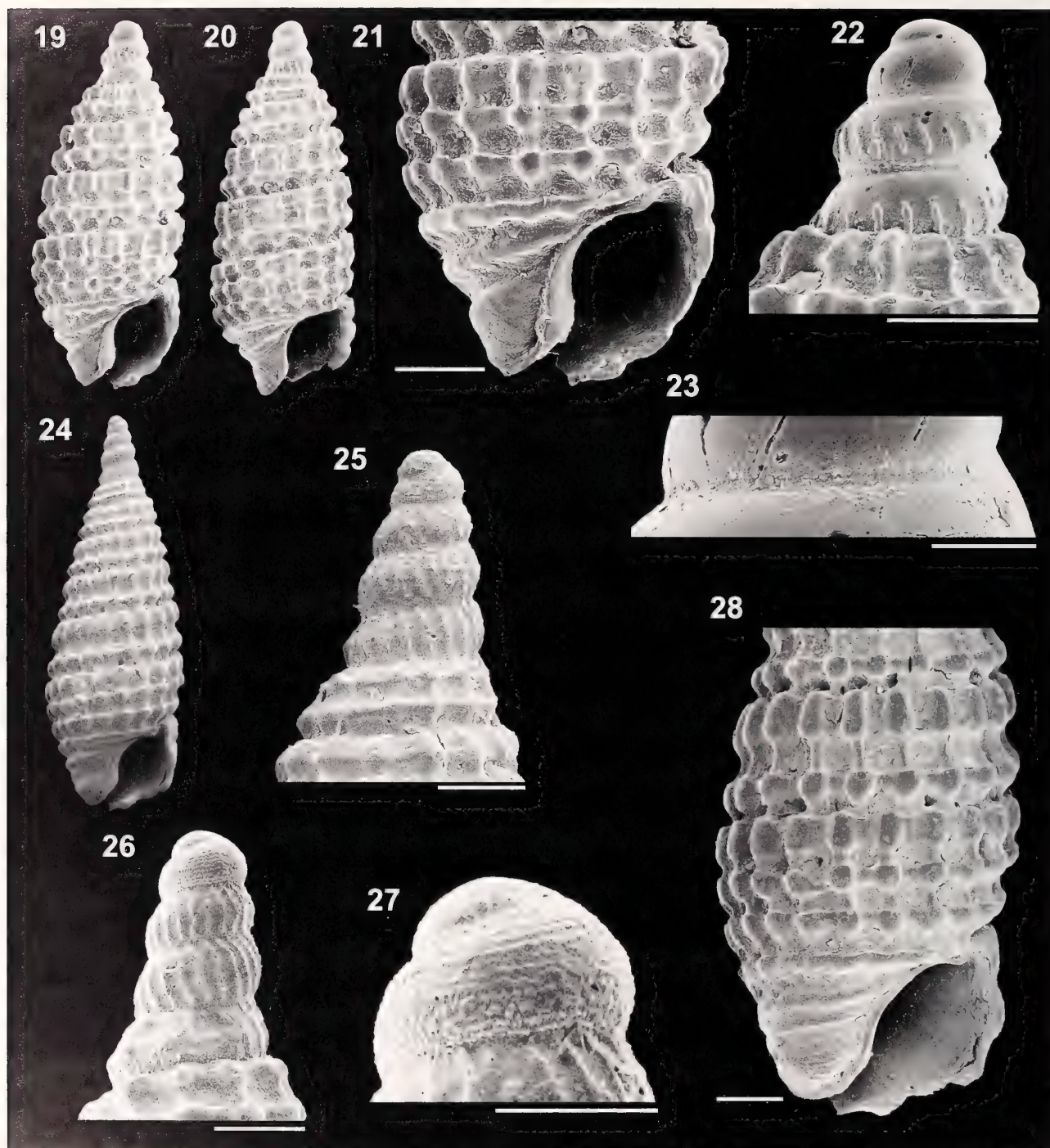
(24°17.129'S, 44°12.149'W, 163 m), off São Paulo state; MNRJ 10981, [1] PADCT sta 6577 (25°15.76'S, 45°04.62'W, 124 m), off São Paulo state; MZSP 86308 [1], PADCT sta 6595 (26°23'S, 46°39'W, 175 m), off Santa Catarina state.

Type locality: off São Paulo state, southeast coast of Brazil (24°17.129'S, 44°12.149'W, 163 m).

Etymology: From Latin Balaustum = balauster. The species is named after its protoconch sculpture, whose series of axial riblets resembles the architectural elements of a balustrade.

Diagnosis: protoconch with small axial riblets restricted to the middle portion of each whorl, not touching the suture; first teleoconch whorls with the two adapical rows of nodules fused together and becoming separated on the subsequent whorls.

Description: shell small, reaching 2 mm of height, somewhat pupiform, opaque. Protoconch subcylindri-



Figures 19–23. *Cerithiopsis balaustium* n.sp. 19, 21–23. holotype (MZSP 86307); 20. paratype (IBUFRJ 15223); 19–20. whole shells (respective lengths: 1.3 mm, 1.4 mm); 21. last whorl; 22. protoconch; 23. detail of protoconch sutural area. Scale bars: 21–22: 200 µm; 23: 50 µm.

Figures 24–28. *Cerithiopsis capixaba* n.sp. 24–25, 28. holotype (IBUFRJ 15221); 26–27. paratype (MZSP 86309); 24. whole shell (length: 2.5 mm); 25–26. protoconchs; 27. detail of early protoconch whorls; 28. last whorl. Scale bar: 25–27: 200 µm; 28: 100 µm.

cal, dark yellow, with about 3.5 whorls of convex outline, the first one dome-shaped; two abapical whorls with small prosocline axial riblets which are restricted to the middle area of the whorls, without reaching the suture, except in its last half-whorl; sutural area with granules, especially on its adapical region, which become thicker and coalescent on the third whorl, forming a small spiral suprasutural cord. Teleoconch with up to five whorls; color varying from light to dark yellow. Suture well impressed. Teleoconch whorl sculpture formed by three spiral cords and about 16 axial ribs on the fourth whorl with the formation of rounded nodules on the intersections; early whorls with the two posterior cords fused together, their nodules appearing to be a single row of bilobate ones, these cords gradually separate from each other in the subsequent whorls until they are equidistant on the last one. Base short, with a slightly nodulose spiral cord on its periphery and two large spiral grooves, separated by a spiral cord, axial growth lines, and thin spiral lines in its anteriormost portion. Aperture somewhat elliptical, with a short siphonal canal. Outer lip thickened.

Cerithiopsis capixaba n.sp

(Figures 24–28)

Type material: holotype: IBUFRJ 15221, [1] REVIZEE sta vv21 (20°38'S, 40°00'W, 33 m), off Espírito Santo state, 26/ii/1996, NOAN coll.; paratypes: IBUFRJ 9275, [1] REVIZEE sta c63 (19°40'42"S, 38°08'15"W, 61 m), off Espírito Santo state, 25/iv/1996, NOAN coll.; IBUFRJ 14138, [2] REVIZEE sta vv38 (19°44'S, 38°22'W, 71.4 m), off Espírito Santo state, 29/ii/1996, NOAN coll.; MNRJ 10982, [3] REVIZEE VI sta y7 (77 m); MZSP 86309, [1] REVIZEE sta 6662 (24°00.946'S, 43°55.540'W, 135 m), off São Paulo state.

Type locality: off Espírito Santo state, southeast coast of Brazil (20°38'S, 40°00'W, 33 m).

Etymology: “Capixaba” is the common denomination given to natives of the state of Espírito Santo, in southeastern Brazil.

Diagnosis: protoconch with many thin axial ribs covering the entire surface of each whorl; early teleoconch whorls with the two adapical rows of nodules fused together and becoming separated on the subsequent whorls.

Description: shell small, reaching 3 mm of height, pupiform with a somewhat acuminate apex, opaque. Protoconch cylindrical, yellow, with about 5 whorls of convex outline, the first one dome-shaped; first two whorls with small granules organized in spiral rows, subsequent whorls with prosocline axial riblets reach-

ing the suture. Teleoconch with up to seven whorls; color light caramel. Suture well impressed. Teleoconch whorl sculpture formed by three spiral cords and about 16 axial ribs on the sixth whorl with the formation of rounded nodules on the intersections; early whorls with the two posterior cords fused together, their nodules appearing to be a single row of bilobate ones, these cords gradually separate from each other in the subsequent whorls until they are equidistant on the sixth whorl. Base very short, with a spiral cord on its periphery and two large spiral grooves, separated by a spiral cord; axial growth lines, and spiral lines in its anteriormost portion. Aperture subquadrate, with a short siphonal canal. Outer lip thickened.

DISCUSSION

Marshall (1978), studying the Cerithiopsidae from New Zealand, considered several genera apart from *Cerithiopsis*, such as *Joculator*, *Horologica*, *Prolixodens*, among others. The distinction among these generic names was based on a combination of teleoconch shape and sculpture, as well as on protoconch type.

In a similar way, Jay & Drivas (2002) considered several generic names, but relied mainly on protoconch characteristics to restrict the concept of *Cerithiopsis* to shells with smooth or punctated protoconchs, along with the genera *Joculator* and *Horologica*. The distinctions among these three genera were related to the general shape of the shell and the base, and the number of spiral nodulose rows per whorl. Species with sculptured protoconchs, on the other hand, were assigned to the genera *Dizoniopsis* Sacco, 1895, *Mendax* and *Prolixodens*. However, the concept adopted for some genera, such as *Mendax*, are not in accordance with those used by Marshall (1978), who regarded *Mendax* as species with lecithotrophic larval type of few (2 ½) whorls, with non-granulated earlier whorls. The species included by Jay & Drivas (2002) have 3–4 whorls (planktotrophic type), with granulated earlier whorls.

Furthermore, Marshall (1978) stated that classifications based on protoconch types do not reflect phylogeny, since there can be genera with both kinds of development (i.e., planktotrophic and lecithotrophic), reflecting different protoconch sculpture patterns.

In the absence of radular and/or anatomical data, we used *Cerithiopsis* in a wide sense to encompass both smooth or axially sculptured protoconchs, a position adopted by Rolán & Espinosa (1995). Also, we recognized no distinction between *Cerithiopsis* and *Joculator*, because the differences among them are related to general shell shape, which is quite variable in some species of *Cerithiopsis*.

Cerithiopsis s.l. species are generally characterized by teleoconch sculpture of three or two rows of nodulose

cords, nearly equidistant, on each whorl. In some species, however, the two adapical nodulose rows are very close to each other, and quite distant from the abapical row; in some cases, these two adapical rows may be fused in a kind of double row, or even only one row may be visible, especially on earlier teleoconch whorls. Marshall (1978) included species with this teleoconch sculpture in *Horologica*, defined as teleoconchs with two spiral cords, a third emerging by fission and subsequent development of the first spiral cord. However, Marshall (1978) himself expressed doubt as to whether *Horologica* would prove to be a subgenus of *Joculator* after eventual forthcoming anatomical data. This suggests to us that the number and disposition of spiral cords are also insufficient to discriminate among generic entities, and again, we have considered *Cerithiopsis* in a broad sense.

Typical western Atlantic representatives of the type of sculpture described above, are *Cerithiopsis fusiformis* (C. B. Adams, 1850) (Figures 1–5), from Jamaica; and *Cerithiopsis aimen* (Figures 6–11) and *Cerithiopsis prieguei* (Figures 12–18), both from Cuba, described by Rolán & Espinosa (1995). These three species are herein reported for the first time from the Brazilian coast.

Rolán & Espinosa (1995) stated that the protoconch of *C. fusiformis* seems smooth, but has a spiral angulation in its middle and, in some specimens, an additional spiral cord near the suture. Some level of erosion may be responsible for this variation. These protoconch characters are visible in the Brazilian specimens (Figures 3, 4).

Cerithiopsis aimen (Figures 6–11) can be distinguished by its smooth protoconch, which lacks any spiral sculpture (Figures 7, 10, 11). In addition, as discussed by Rolán & Espinosa (1995), *C. aimen* also differs from *C. fusiformis* in the arrangement and relative size of the nodules on the first teleoconch whorl. The first teleoconch whorl of *C. aimen* has three, equally spaced, nodulose rows, the middle one smallest, until the second teleoconch whorl, when the two upper rows become fused (Figures 7, 10, 11). In *C. fusiformis*, the adapical row is smaller than the other two and is already closer to the middle row from the beginning of the teleoconch (Figures 3, 4).

Cerithiopsis prieguei (Figures 12–18) displays the same sculptural pattern on the first teleoconch whorl (Figures 16, 17) as *C. fusiformis*. The easiest way to distinguish this species from the others is by the protoconch sculpture, which has two fine, spiral cords, with small, incomplete, oblique axial ribs (Figures 16, 17). Further, the sutural area of the protoconch has some small granules (Figure 18).

Besides the three species mentioned above, this paper presents the description of two new species, with similar shell shape and sculpture pattern. Both *Cerithiopsis*

balaustium and *Cerithiopsis capixaba* have the adapical row smaller than the other two at the beginning of the teleoconch, similar to *C. fusiformis*. Particularly in *Cerithiopsis balaustium* the adapical rows of nodules are extremely close since the first whorl.

The teleoconch whorls of the species studied are very similar, though their shapes are not exactly the same: *Cerithiopsis balaustium* (Figures 19, 20) is somewhat globose and smaller than the others, whereas *Cerithiopsis capixaba* (Figure 24) is somewhat pear-shaped, and *C. fusiformis* (Figures 1, 2), *C. aimen* (Figures 6, 8) and *C. prieguei* (Figures 12–14) are oval. Still, in our opinion, this trait is too variable and hardly sufficient to allow a proper identification of these species.

There are also slight differences in the separation of the adapical rows of nodules. In *C. fusiformis*, *C. aimen*, *C. prieguei* and *C. capixaba*, the rows become separated in the fifth or sixth whorls only; whereas in *C. balaustium* the two fused spiral cords are already separated by the fourth whorl (Figures 19, 20).

It is clear, though, that among the conchological characters, the sculpture on the protoconch is the most reliable and conclusive when telling these species apart. All the species have protoconchs of the planktotrophic type, with four or five whorls. Marshall (1978) stated that, although not reliable for generic classification, differences in sculpturing of the planktotrophic protoconch may be used for species discrimination, because species with this larval development are usually intraspecifically constant.

The protoconch of *Cerithiopsis balaustium* has short axial cords that do not touch the suture (Figures 22, 23), whereas that of *Cerithiopsis capixaba* has five whorls, the two adapical finely granulose and the remainder with axial cords touching the suture above and below (Figures 25–27). The protoconch sculpture of *C. balaustium* is somewhat similar to that of *Prolixodens sknips* Jay & Drivas, 2002, but in this species, which occurs in the Indian Ocean, the axial riblets are more prominent; besides, the teleoconch does not have the two fused adapical rows in the adapical whorls. A recently described species from Cuba, *Cerithiopsis apexcostata* Rolán, Espinosa & Fernández-Garcés (2007) has a very similar protoconch sculpture, but in this species, the axial cords, touch the suture below, while in *C. balaustium*, the cords are, in most of the protoconch whorls restricted to the middle area of the whorl. Also, in *C. apexcostata*, the two posterior cords in the teleoconch whorls never fuse together, as occurs in the three older whorls of *C. balaustium*.

Also, for *C. capixaba*, a similar protoconch can be found in three species from the Indian Ocean, *Mendax penneyi*, *Mendax mascarenensis* and *Mendax ribesae*, all described by Jay & Drivas (2002); however, the teleoconch shapes and sculpturing are markedly

different. Rolán et al. (2007) described and illustrated the protoconch of *Cerithiopsis ara* Dall & Bartsch, 1911, with 4 ¼ whorls, the first one with spiral cords and the subsequent with axial ribs crossed by small spiral threads; this is very similar to the protoconch of *C. capixaba*, but in the species from Brazil, the spiral cords in the initial whorls are formed by small granules organized in spiral rows, and in the subsequent whorls, there are no spiral threads. The most important difference between the two species, however, is in the general shell shape, elongate and with an acuminate apex in *C. capixaba* and short and pupoid in *C. ara*.

Cerithiopsis prieguei has a protoconch ornamented with small granules at the sutural area of the two earlier whorls and two spiral cords connected by thin prosocline axial riblets on the two abapical whorls (Figures 16–18). The protoconchs of *C. fusiformis* (Figures 3, 4) and *C. aimen* (Figures 7, 10, 11) are generally smooth, although on the protoconch of *C. fusiformis*, there is a small spiral keel in the middle on the two abapical whorls; similar spiral keels can be found in the protoconchs of *Cerithiopsis beneitoi* Rolán, Espinosa & Fernández-Garcés, 2007 and *Cerithiopsis dilata* Rolán, Espinosa & Fernández-Garcés, 2007.

Olsson & Harbison (1953) described *Cerithiopsis aralia*, from the Pliocene north of St. Petersburg, Florida, and stated that this species should be carefully compared with *Cerithiopsis fusiformis*. Jong & Coomans (1988) considered *Cerithiopsis brassica* Olsson & Harbison, 1953 as a synonym. We examined the holotype of *C. aralia*, and although both species are very similar, we prefer to retain them as separate taxa because we feel that additional studies are necessary to confirm the possible synonymy of species from such distant geological provenance. Although we did not examine the holotype of *C. brassica*, the same interpretation applies.

The previously known distribution of *C. fusiformis* included the Western Atlantic, from North Carolina (U.S.A.) to the Caribbean (Rosenberg, 2005); *C. aimen* and *C. prieguei* were known only from Cuba (Rolán & Espinosa, 1995). This is, therefore, their first record from the South Atlantic. In Brazil, *C. fusiformis* is widely distributed, from the states of Pernambuco (northeastern Brazil, $\cong 8^\circ\text{S}$) to Rio Grande do Sul (southern Brazil, $\cong 30^\circ\text{S}$); *C. prieguei* and *C. aimen* have only been found in southeastern Brazil (Espírito Santo State, $\cong 19^\circ\text{S}$). Both *Cerithiopsis balaustium* and *Cerithiopsis capixaba* are restricted to localities in southeastern Brazil: about 24°S and 20°S – 24°S , respectively, with some records of *Cerithiopsis balaustium* from the northeast coast, though in a southern locality ($\cong 13^\circ\text{S}$).

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A Record of the Invasive Slug *Veronicella cubensis* (Pfeiffer, 1840) in California

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Abstract. *Veronicella cubensis* (Pfeiffer, 1840) is reported from California for the first time and the significance of the find in terms of agricultural production and the effectiveness of invasive gastropod screening at air and seaports within the state are discussed.

Following a survey of the invasive slug fauna of California, we present the first record of *Veronicella cubensis* (Pfeiffer, 1840) (Stylommatophora: Veronicellidae) on the west coast of North America. A single individual was collected under a potted plant in a garden center in Santa Barbara, California (N34°24'908", W119°45.018") on 19th June 2006. Other slug species collected in the same location were *Deroceras reticulatum* (Müller, 1774), *Deroceras panormitanum* (Lessona and Pollonera, 1882), *Lehmannia valentiana* (d'Audebard de Féussac, 1823) and *Arion hortensis* d'Audebard de Féussac, 1819. The specimen has been deposited at Department of Malacology, Academy of Natural Sciences in Philadelphia under catalogue number ANSP-A21201.

Although having a highly variable coloration (including an albino form), the notum of *V. cubensis* is usually dark to pale brown (Figure 1), generally with a pale dorsomedian line. It often has black speckling which sometimes fuses to form two lateral bands (Robinson and Hollingsworth, 2004). The female genital pore is located closer to the pedal sulcus than the peritoneum. The penis has a characteristic flaring that produces a blade-like structure down each side and the penial gland has numerous, very long tubules (David G. Robinson, pers. comm.).

It is thought that *V. cubensis* is native to Cuba (Robinson and Hollingsworth, 2004) but it has also been introduced to Jamaica (Baker, 1925), Bahamas, Haiti, Dominican Republic, Puerto Rico, Guam (Thomé, 1993a), Antigua, Saint Kitts and Nevis, Dominica, Barbados (West Indies), St. Coix, Olosega (Manu 'u Islands), Tutuila (American Samoa), Pohnpei (Micronesia), Rota, the Northern Mariana Islands (Robinson and Hollingsworth, 2004) and Hawai'i (Thomé, 1993b). It has also been previously collected (interceptions) in Florida and New Orleans (Thomé, 1993a).

In 2002, *V. cubensis* was listed as the seventh most

potentially damaging gastropod of either agriculture or natural ecosystems if it became established in the U.S. (Cowie, 2002). Since this species was introduced into Hawai'i in 1985, it has caused severe damage to vegetable, ornamental, and landscape plants, and the species is now a potential threat to Hawai'i's \$104 million vegetable and floriculture industry (Hata et al., 1997). The species is also an extremely serious agricultural and horticultural pest on Rota and Guam (Robinson and Hollingsworth, 2004). In addition, *V. cubensis* has been associated with the transmission of the trematode *Angiostrongylus cantonensis* (Chen) which causes the potentially lethal eosinophilic meningitis in humans (Cuba: Aguiar et al., 1981; Jamaica: Lindo et al., 2004).

Although our record is of a single specimen and return trips to the same location and surrounding areas on 2 August 2006 and 14 March 2007 did not yield any additional individuals, our discovery is still of concern as it indicates that some potentially severe pest gastropods are not being detected during pre-clearance at U.S. seaports, airports and border crossings. Such failed interceptions represent the first step in establishment of exotic species in the U.S. and as such these finds should be reported as they may help to prevent further invasions and the ultimate establishment of pestiferous species. Although some species may not be of concern at their port of entry, they represent a source for transport to other areas of the U.S. and the world, where they could potentially become established and become serious pests. In the case of *V. cubensis*, spread of individuals to areas such as New Orleans could result in such a scenario. In addition, *V. cubensis* is predominantly a tropical to subtropical species (Gomes and Thomé, in press) and heavily-irrigated desert areas in southern California, including extensive and diverse urban landscape environments, may be a vulnerable habitat for colonization, as they are likely to provide the hot, humid conditions favored by tropical gastropods



Figure 1. Specimen of *Veronicella cubensis* (Pfeiffer, 1840) collected in Santa Barbara, California.

such as *V. cubensis*. It is therefore imperative that improved screening of shipments that are known to harbor invasive slugs and snails e.g., tiles, fruit, vegetables and ornamentals (Robinson, 1999) are put in place to help mitigate the problem of invasive gastropods in the U.S.

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Developmental Mode in Opisthobranch Molluscs from the Tropical Eastern Pacific Ocean

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Abstract. Little has been published on mode of development in benthic opisthobranchs from the tropical eastern Pacific Ocean. Based on observations of uncleaved eggs, developing embryos, or hatching larvae, we determined or inferred mode of development for 43 species collected primarily from Bahía de Banderas, México. Forty-two of these, including the umbraculoidean *Tylodina fungina*, had planktotrophic development, while *Phidiana lasercrucensis* hatched as lecithotrophic larvae. Both the sacoglossan *Elysia pusilla*, which had small eggs, relatively large egg capsules, and irregular strands of extra-capsular yolk in its egg mass, and the dendronotacean *Lomanotus vermiformis* may also have lecithotrophic development in this region. Combined with previously existing data, mode of development is now known for 91 species of native, benthic, shallow-water opisthobranchs from the eastern Pacific and can be tentatively inferred for another 13 species based on data from other regions. Four species hatch as lecithotrophic larvae, and the remaining 100 as planktotrophic larvae. The prevalence of planktotrophic development in opisthobranchs from the eastern Pacific is similar to that known from the adjacent northeast Pacific Ocean, but is higher than in the less productive waters of the Caribbean Sea and the tropical western Atlantic Ocean, where opisthobranch eggs attain much larger diameters and 37% of the 112 species examined have either lecithotrophic or direct development. These results agree with those known for a diverse range of marine invertebrates across the Isthmus of Panama and are consistent with evolutionary trends expected in the egg size and mode of development with historical changes in ocean productivity and larval feeding environment.

INTRODUCTION

More than 90% of 126 native species of opisthobranchs studied from the cool temperate waters of the northeast Pacific Ocean have planktotrophic development, a high prevalence thought to reflect the region's suitability for larval feeding and growth, especially its generally slow currents, large geographic expanse, and primary production driven by coastal upwelling and horizontal advection via the California Current, (Goddard, 2004). In contrast, relatively little information has been published on developmental mode in opisthobranchs from the tropical eastern Pacific (hereafter E Pacific), which includes the Panamic biogeographic province and extends from southern Baja California Sur to central Peru (Briggs, 1974). Here we document developmental mode in 43 species of shallow-water opisthobranchs known from the Pacific coast of Mexico, and compare the frequencies of the major modes of development to those known from the NE Pacific as well as the neighboring Caribbean Sea and

greater tropical western Atlantic Ocean (together referred to hereafter as the W Atlantic).

Based on the distributions reported recently by Behrens & Hermosillo (2005), Camacho et al. (2005) and Hermosillo et al. (2006), 17 species included in Goddard (2004) have ranges extending well into the Panamic province. Excepting *Antaeolidiella indica* (Bergh 1888), which has lecithotrophic development and is circumtropical in distribution, all have planktotrophic larval development. Gonsalves-Jackson (2001, 2004) compared development in opisthobranchs across the Isthmus of Panama, and observed "planktonic" development in all 39 Pacific species she studied. Although Gonsalves-Jackson (2004) did not distinguish between planktotrophy and pelagic lecithotrophy, the small egg-sizes she reported (under 70 microns for sacoglossans and under 115 microns for all other species), combined with her descriptions and illustrations of embryos and hatching larvae, reliably indicate planktotrophic development for all 39 species, based on morphological criteria and known egg-size distribu-

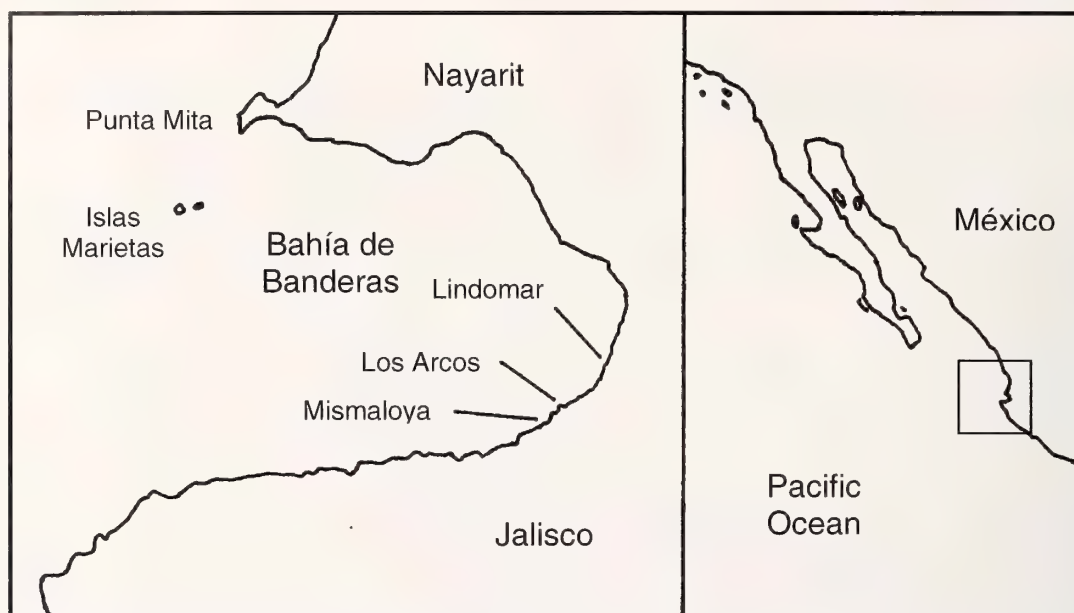


Figure 1. Map of Bahía de Banderas, México, showing collection localities.

tions (Thompson, 1976; Bonar, 1978; Hadfield & Miller, 1987; Goddard, 2004). Finally, information on the development of 13 of the more widely distributed Panamic opisthobranchs has been obtained from other regions of the world. Owing to the possibilities of geographic divergence and poecilogony, these latter data cannot be considered definitive for the E Pacific, but do suggest that *Lomanotus vermiformis* Eliot 1908 and *Phestilla lugubris* (Bergh 1870) have lecithotrophic development, and that the remaining 11 species are planktotrophic (Harris, 1975; Bandel, 1976; Clark & Goetzfried, 1978; Switzer-Dunlap, 1978; Schmekel & Portmann, 1982; Gonsalves-Jackson, 2004; Table 1). Taken together, these data suggest that the prevalence of planktotrophy in the E Pacific is similarly high to that observed in the NE Pacific.

To better compare developmental mode in opisthobranchs from the two regions, we present here data on the development of 45 species of opisthobranchs from the Panamic biogeographic province. We then compare our results from the E Pacific to those from the more seasonally stable and relatively oligotrophic waters of W Atlantic, where a shift toward larger egg sizes and benthic or non-planktotrophic modes of development has been documented in opisthobranch gastropods (Gonsalves-Jackson, 2001, 2004), as well as other taxa, including bivalve molluscs, crustaceans, echinoid echinoderms, and bryozoans (Lessios, 1990; Jackson & Herrera, 1999; Marko & Moran, 2002; Wehrtmann & Albornoz, 2002; Fortunato, 2004; Moran, 2004).

During our survey, we were able observe the egg masses and hatching larvae of the umbraculoidean

opisthobranch *Tylodina fungina* Gabb, 1865. Because so little is known about the development and larvae of umbraculoideans (see Gibson, 2003), we also provide here a detailed description of its egg mass and hatching larvae.

METHODS

Adult opisthobranchs and opisthobranch egg masses positively identified in the field were collected by hand from 16–28 February 2006 from subtidal and intertidal sites within Bahía de Banderas (20°30'N, 105°30'W), in the states of Jalisco and Nayarit, on the west coast of Mexico (Figure 1). This bay, approximately the size, shape and depth of Monterey Bay, California, and the collecting localities, have been described by Hermosillo (2003). Local sea surface temperatures during our work period averaged approximately 21°C. Adults were held in the field laboratory in containers (250 to 2000 ml) of seawater at 19–23°C until they laid egg masses. Recently laid egg masses were examined using a compound microscope equipped with an ocular micrometer. If first cleavage had not commenced, the diameters of a random sample of 10 zygotes were measured in each egg mass; otherwise, an upper limit on zygote size was estimated by measuring the dimensions of a few randomly selected embryos at or before the gastrula stage and (or) the minimum dimension of tightly fitting egg capsules containing embryos at or before the gastrula stage of development. After initial examination, each egg mass (or a portion of a large egg mass) was then isolated in a separate, labeled vial. The seawater in these vials was changed

daily, and the egg masses examined daily for hatching. Hatching larvae were then examined, measured and in some cases photographed. Developmental mode (planktotrophic, lecithotrophic and direct) and larval shell type (coiled type 1 and egg-shaped, inflated type 2) were assigned according to the egg size distributions and larval morphological criteria described by Thompson (1961, 1976), Bonar (1978), Clark & Jensen (1981), Hadfield & Switzer-Dunlap (1984), Hadfield & Miller (1987) and Goddard (2004). After obtaining the above egg masses, most of the adult specimens were relaxed in 7.5% $MgCl_2$, fixed in 70% ethanol, and deposited as voucher specimens in the California Academy of Sciences. Other adults were returned alive to the field. We used an underwater data logger (StowAway Tidbit, Onset Computer Corp.) to record temperature at 10 min. intervals in our holding containers.

We estimated egg size for *Polycera alabe* (COLLIER & FARMER 1964) and late embryo size for *Lomanotus vermiformis*, by placing a mm scale bar next to egg masses in the field and taking underwater digital images. Additional data, obtained by the senior author in central and southern California and Baja California, (1) supplement the data for three species we collected in Bahía de Banderas, and (2) are given for six additional species whose geographic ranges include the Panamic province.

To compare frequencies of development modes in the E Pacific to those in the NE Pacific and the W Atlantic, we assigned developmental mode (according to the criteria mentioned above) using published data on species from the E Pacific, and then combined these results with our own. We then calculated the frequencies of the different modes of development for (1) the NE Pacific based on Goddard (2004, 2005), and Krug et al. (2007); and (2) the W Atlantic based on data and determinations of developmental mode in Bandel (1976), Clark & Goetzfried (1978), Eyster (1980, 1981), Clark & Jensen (1981), DeFreese & Clark (1983), Carroll & Kempf (1990), Cronin et al. (1995), Ortea (2001), Gonsalves-Jackson (2004), and Pierce et al. (2006). For 17 species from the W Atlantic we assigned mode of development as either planktotrophic or direct based on close-up images of egg masses with either small or large eggs/embryos in Valdés et al. (2006); our determinations for six of these species were confirmed by information in the other references cited above for the W Atlantic, giving us confidence that our determinations for the other 11 species (for which no other information exists) were accurate. Ortea (2001) listed egg sizes for 11 Caribbean species of the nudibranch genus *Doto*, but provided no information on hatching stages or type of development. For six of these species we assigned developmental mode based on the egg-size distributions known for each mode, conservatively considering species with eggs less than

100 μm in diameter as planktotrophic, species with eggs greater than 165 μm diameter as lecithotrophic, and those with eggs greater than 220 μm as direct developers. To avoid tabulating Atlantic species more than once, we used Valdés et al. (2006) and the Sea Slug Forum (<http://www.seaslugforum.net/>) to check for synonymies and recent taxonomic revisions.

We used JMP (version 7.0, SAS Institute, Inc.) to (1) conduct contingency analyses of the frequencies of planktotrophic vs. non-planktotrophic (lecithotrophic and direct) development by region, and (2) compare egg size distributions by region. For the latter we excluded egg size data obtained outside the regions of interest, but used all other determinations of egg size available from the above sources, even if mode of development is unknown. Owing to (1) the large number of species of opisthobranchs from the W Atlantic found to have non-planktotrophic development, and (2) the lack of detailed phylogenies for most opisthobranch taxa across the Isthmus of Panama, we limited the contingency analysis of developmental mode by E Pacific vs. W Atlantic Oceans to the numbers of families, rather than species, with planktotrophic vs. non-planktotrophic development. To reduce the influence of phylogenetic constraints unique to particular families, we further limited this analysis to families common to both oceans.

RESULTS

We found 70 species of opisthobranchs in Bahía de Banderas and obtained data on the development of 39 of these. Combined with the data on six Panamic species obtained by the senior author outside of Bahía de Banderas, data on development were obtained for a total of 45 species (Table 1). Forty-two had planktotrophic development, and the aeolid nudibranch *Phidiana lascrucensis* Bertsch & Ferreira 1974 had lecithotrophic development (Table 1). Although we obtained data on the egg and embryo size, respectively, of the sacoglossan *Elysia pusilla* (Bergh 1872) and dendronotacean nudibranch *Lomanotus vermiformis* (Table 1), we did not observe their hatching stages and were unable to determine with certainty their mode of development. The former had small eggs but had relatively voluminous egg capsules surrounded by irregular strands of extra-capsular yolk (ECY) (Figure 2). As shown by Clark & Jensen (1981), the presence of these traits can indicate lecithotrophic or even direct development in sacoglossans, despite otherwise small egg size. The embryos of *Lomanotus vermiformis* observed in the field were large enough (Table 1) that none of the three major modes of development can be ruled out based solely on known distributions of egg size and shell size at hatching (Hadfield and Miller, 1987; Goddard, 2004). Clark &

Table 1

Comparative data on embryonic development in opisthobranchs known from the tropical eastern Pacific Ocean. Each row of data was obtained from a single egg mass, either collected in the field or deposited in the laboratory, with a dash (—) representing no data collected. Unless specified otherwise, all localities are in Bahía de Banderas, Jalisco and Nayarit, Mexico (see Figure 1). Mode of development: P, planktotrophic; L, lecithotrophic. If hatching larvae were not observed, mode of development was inferred based on the egg size distributions reported by Hadfield and Miller (1987) for the major modes of development, and comparisons with congeners (see Goddard, 2004). Inferred modes of development are in parentheses. Values for egg diameter and shell length at hatching are means, plus or minus one standard deviation, with sample size in parentheses. In cases in which zygotes were not observed, an upper limit for egg size is given, based on measurements of early embryonic stages (16 cell through gastrula), which are typically a little longer in greatest dimension than the zygotes (personal observations; see Methods). Temperature was recorded only in the laboratory and is given only for egg masses held for most or all of the embryonic period; sea-surface temperatures at our study sites in Mexico in February 2006 were approximately 21°C.

Taxon	Egg diameter (μm)	# eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell type	Shell length at hatching (μm)	Eyespots at hatching	Mode of develop- ment	Locality
Cephalaspidea									
<i>Haminoea virescens</i> (Sowerby 1833)	—	1	—	—	1	144.1 \pm 4.7 (5)	no	P	Santa Barbara, California
CASIZ 174985	—	1	—	—	1	100.9 \pm 4.7 (5)	no	P	Punta Mita
<i>Haminoea ovalis</i> Pease 1868	<81	1	—	—	—	—	—	(P)	Punta Mita
<i>Navanax aenigmaticus</i> (Bergh 1893)	—	—	—	—	—	—	—	—	—
Anaspidea									
<i>Phyllaplysia padinae</i> Williams & Gosliner 1973	<100	1	—	—	—	—	—	—	Lindomar
CASIZ 174105	—	1	—	—	1	121.4 \pm 3.4 (10)	no	P	Bahía de Los Angeles, Baja California
Umbraculoidea									
<i>Tylodina fungina</i> Gabb 1865	73 ^a	1	—	20–23	1	126.0 \pm 3.7 (5)	no	P	Los Arcos, subtidal
CASIZ 174054 (egg mass)	—	—	—	—	—	—	—	—	—
Sacoglossa									
<i>Elystia diomedea</i> (Bergh 1894)	<65	1	—	—	1	128.4 \pm 2.4 (10)	no	P	Punta Mita
<i>Elystia pusilla</i> Bergh 1872	—	—	—	—	—	—	—	(L?) ^b	Punta Mita
CASIZ 174092	<73	1	—	—	—	—	—	(P)	Los Arcos, intertidal
<i>Oxynoe panamensis</i> Pilsbry & Olsson 1943	—	—	—	—	1	96.4 \pm 2.9 (2)	no	P	Los Arcos, intertidal
CASIZ 174085	—	—	—	—	—	—	—	—	—
<i>Polybranchia viridis</i> (Deshayes 1857)	—	—	—	—	—	—	—	—	—
CASIZ 174098	—	—	—	—	—	—	—	—	—
Nudipleura: Pleurobranchidae									
<i>Berthellina ilisima</i> Marcus & Marcus 1967	—	6–9	—	—	1	144.5 \pm 0.4 (2)	yes	P	Santa Barbara, California
<i>Pleurobranchus areolatus</i> (Mörch 1863)	—	—	—	—	1	121.4 \pm 3.1 (10)	no	P	Los Arcos, intertidal
Nudipleura: Doridina									
<i>Conualevia alba</i> Collier & Farmer 1964	87.7 \pm 1.4 (10)	1	15–16	16–19	1	150.7 \pm 2.5 (10)	no	P	Monterey, California
CASIZ 174704	90.1 \pm 1.0 (10)	1	—	—	—	—	—	—	—
<i>Dendrodoris fumata</i> (Rüppell & Leuckart 1831)	—	1	—	—	—	151.2 \pm 3.4 (10)	no	—	—
CASIZ 174096	101.6 \pm 0.7 (5)	1	—	—	1	174.8 \pm 4.8 (10)	no	P	Mismaloya

Table 1
Continued.

Taxon	Egg diameter (μm)	# eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell type	Shell length at hatching (μm)	Eyespots at hatching	Mode of develop- ment	Locality
<i>Diatula aurila</i> (Marcus & Marcus 1967) CASIZ 174061, 174101	87.9 \pm 2.6 (10)	1–2	15	16–19	1	139.6 \pm 5.7 (10)	no	P	Punta Rosarito, Baja California ^c Lindomar
<i>Doriopsilla rowena</i> Marcus & Marcus 1967 CASIZ 174055	97.4 \pm 3.1 (3)	1	—	—	—	—	—	(P)	Mismaloya
<i>Doris granulosa</i> (Pease 1860) CASIZ 174061	<73	1	—	—	—	—	—	(P)	Punta Mita
<i>Doris immonda</i> (Risbec 1928) CASIZ 174084	67.4 \pm 1.2 (10)	1	—	—	—	—	—	(P)	Lindomar
<i>Jorunna</i> sp. 1 of Behrens & Hermosillo 2005 CASIZ 174099	<65	1	—	—	—	—	—	(P)	Punta Rosarito, Baja California
<i>Okenia angelensis</i> Lance 1966 CASIZ 174104	\approx 62 ^d	1	—	—	—	—	—	(P)	Mismaloya
<i>Okenia angelica</i> Gosliner & Berstch 2004 CASIZ 174093	<68	1	4	19–23	1	103.5 \pm 1.9 (10)	no	P	Bahia de Banderas Marietas
<i>Polycera alabe</i> Collier & Farmer 1964 <i>Tambjia eliora</i> Marcus & Marcus 1967 CASIZ 174087	\approx 60 ^e —	1 1	— 7	— 19–23	— 1	— 129.4 \pm 2.5 (10)	— no	(P) P	Marietas
<i>Thoridisa</i> sp. 1 of Behrens & Hermosillo 2005 CASIZ 173057	<80 <80	1 1	5 6	19–23 19–23	1 1	120.5 \pm 4.7 (5) 127.4 \pm 2.1 (10)	no no	P P	Los Arcos, intertidal
<i>Tyrinna evelinae</i> (Marcus 1958) CASIZ 174083	<81	1	—	19–23	1	\geq 118 ^f	no	P	Mismaloya
Nudipleura: Dendronotina <i>Doto</i> sp. 2 of Behrens & Hermosillo 2005 CASIZ 174090	<80	1	5	19–23	1	121.4 \pm 4.6 (10)	no	P	Lindomar
<i>Doto</i> sp. 3 of Behrens & Hermosillo 2005 CASIZ 174089	<89	1	—	—	1	127.4 \pm 8.8 (6)	no	P	Los Arcos, intertidal
<i>Doto</i> sp. (brown) CASIZ 174103	<80	1	—	—	1	104.3 \pm 1.8 (2)	no	P	Montana de Oro State Park, California
<i>Hancockia californica</i> MacFarland 1923 CASIZ 174703	99.6 \pm 2.1 (15)	1	10	12–17	2	242.9 \pm 3.0 (20)	no	P	Bahia de Banderas Mismaloya
<i>Lomanotus vermiciformis</i> Eliot 1908 <i>Lomanotus</i> sp. 2 of Behrens & Hermosillo 2005	— 65.0 \pm 1.5 (5) 67.6 \pm 2.0 (5)	— 1 1	— 5 —	— 19–23 —	— 1 1	\approx 190 ^g — —	no? — —	(L?) ^b — —	P
<i>Tritonia pickensii</i> Marcus & Marcus 1967 Nudipleura: Acolidiina <i>Acolidiella alba</i> (Risbec 1928)	<69	1	—	—	1	116.8 \pm 4.2 (10)	no	P	Lindomar
<i>Acolidiella chromosoma</i> (Cockerell & Eliot 1905) CASIZ 174060, 174106	69.7 \pm 0.4 (10) <85 <90	1 — 1	— — 6.5	— — 16–19	— — 1	— — 127.0 \pm 4.3 (10)	— — no	(P) — P	Mismaloya Los Arcos, intertidal Punta Rosarito, Baja California ^c Lindomar
<i>Bajacolis bertschi</i> Gosliner & Behrens 1986 CASIZ 174097	<89	1	—	—	—	—	—	(P)	

Table 1
Continued.

Taxon	Egg diameter (μm)	# eggs per capsule	Embryonic period (days)	Temp. ($^{\circ}\text{C}$)	Shell type	Shell length at hatching (μm)	Eyespots at hatching	Mode of develop- ment	Locality
<i>Cuthona lizae</i> Angulo & Valdés 2003	—	1	3.5	19–23	2	241.0 \pm 6.0 (5)	yes	P	Mismaloya
CASIZ 173058, 174058	88.6 \pm 1.4 (10)	1	—	—	—	—	—	(P)	Los Arcos, intertidal
<i>Eubranchius cucullus</i> Behrens 1985	<100	1	—	—	—	—	—	(P)	Lindomar
CASIZ 173062	—	—	—	—	—	—	—	—	—
<i>Eubranchius</i> sp. 2 of Camacho-Garcia et al. 2005	—	1	—	—	2	227.8 \pm 3.2 (10)	yes	P	Los Arcos, intertidal
CASIZ 174057	—	—	—	—	—	—	—	—	—
<i>Eubranchius</i> sp.	<94	1	4	19–23	2	212.2 \pm 3.2 (5)	yes	P	Los Arcos, intertidal
CASIZ 174094	—	1	—	—	2	203.2 \pm 8.5 (5)	yes	P	—
<i>Favorinus elenalexiae</i> Garcia & Troncoso 2001	<80	1	4	19–23	1	115.0 \pm 1.8 (10)	no	P	Marietas
CASIZ 174060	—	—	—	—	—	—	—	—	—
<i>Flabellina marcusorum</i> Gosliner & Kuzirian 1990	<73	1	—	—	—	—	—	(P)	Lindomar
<i>Flabellina telja</i> Marcus & Marcus 1967	66.1 \pm 0.6 (4)	1	4	19–23	1	123.7 \pm 3.7 (10)	no	P	Mismaloya
CASIZ 174059	—	—	—	—	—	—	—	—	—
<i>Flabellina</i> sp. 1 of Behrens & Hermosillo 2005	<74	1	5	19–23	1	99.6 \pm 4.9 (5)	no	P	Los Arcos, subtidal
CASIZ 173059	—	—	—	—	1	102.2 \pm 1.8 (5)	no	P	—
<i>Hermosita hakanumatata</i> Ortea, Caballer & Espinosa 2003	—	1	—	—	1	115.9 \pm 5.6 (4)	no	P	Marietas
CASIZ 174088	—	—	—	—	—	—	—	—	—
<i>Phidiana lasrucensis</i> Bertsch & Ferreira 1974	<150	1	—	—	—	—	—	—	Punta Mita
CASIZ 174056, 174102	146.6 \pm 1.8 (10)	1	23	14–16	1	248.6 \pm 7.2 (10)	yes	L	Bahia de Los Angeles, Baja California
<i>Spirilla neapolitana</i> (Delle Chiaje 1823)	<77	1–3	—	—	—	—	—	(P)	Lindomar

^a Based on the diameter of two uncleaved eggs in a field-collected egg mass containing embryos at the gastrula stage. Early embryos measured 73 to 85 μm in longest dimension.

^b Observations of hatching veligers are needed to confirm this mode of development (see text).

^c Goddard (2004, unpublished data).

^d Based on measurements of early embryos fixed in 70% ethanol.

^e Estimate based on image of egg mass next to mm ruler taken in field (see Methods).

^f Based on measurements of pre-hatching veligers.

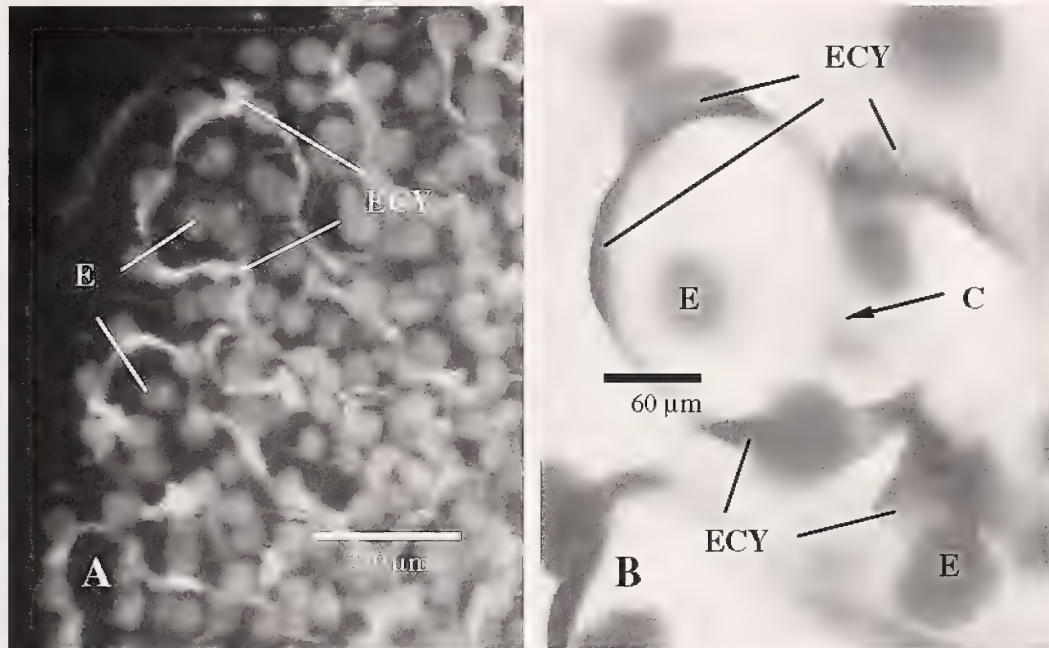


Figure 2. *Elysia pusilla*. A. Detail of egg mass, showing egg capsules (C), extra-capsular yolk (ECY), and embryos (E). B. Close-up of extra-capsular yolk on outside of egg capsules.

Goetzfried (1978) reported that this species has lecithotrophic development in Florida.

We obtained data on the development of nine undescribed species, eight of which are recognized and illustrated in Behrens & Hermosillo (2005), Camacho et al. (2005) or Hermosillo et al. (2006), and one of which (*Eubranchius* sp.) appears to be new. Our record of *Doris immonda* (Risbec 1928) from under coral rubble at Punta Mita, the northern boundary of Bahía de Banderas, is the first sighting of this species in Mexican waters and only the second record of its occurrence outside the Indo-west Pacific (Camacho et al., 2005). Voucher specimens for all ten of these species have been deposited in the California Academy of Sciences (Table 1).

Combined with previously existing data from the region (see Introduction), mode of development is now known for approximately 91 species of native, benthic, shallow-water opisthobranchs from the E Pacific and can be tentatively inferred for an additional 13 species based on published data from other regions. The aeolid nudibranchs *Antaeolidiella indica* and *Phidiana lasrucensis*, and likely also both the dendronotid *Lomanotus vermiformis* and the aeolid *Phestilla lugubris*, hatch as lecithotrophic larvae, and the remaining 100 as planktotrophic larvae (Table 2). Fifteen of the 39 E Pacific species studied by Gonsalves-Jackson (2004) were only identified to genus (with voucher specimens of each deposited in the American Museum of Natural History). Depending on the overlap with species we

studied, this might reduce the total number of E Pacific species whose development is known, but it wouldn't significantly affect the overall prevalence (approximately 4%) of lecithotrophic development known from this region. By number of species, the incidence of planktotrophic vs. non-planktotrophic development in the E Pacific did not differ significantly from that observed in the NE Pacific Ocean (Table 2, Likelihood ratio $\chi^2 = 1.735$, $P = 0.188$).

From the literature we were able to determine or infer mode of development for 112 species of opisthobranchs from the W Atlantic (Tables 2 & 3). Lecithotrophic and direct modes of development were more prevalent in the W Atlantic compared to the E Pacific, comprising 21% and 16%, respectively, of the 112 species. In the W Atlantic these non-planktotrophic or non-feeding modes of development occurred in 17 families (Table 3) from all of the major orders and suborders of benthic opisthobranchs, save the Umbraculida, the development of which has not been examined in the W Atlantic. Sixteen of these families have representatives in the E Pacific, where non-feeding development is known from four and planktotrophic development from all 16 (Table 3). Limiting the contingency analysis to these 16 families, the incidence of non-feeding development, by number of families, is significantly higher in the W Atlantic than in the E Pacific (Likelihood ratio $\chi^2 = 5.830$, $P = 0.016$).

The higher prevalence of non-planktotrophic modes of development in the W Atlantic Ocean, compared to

Table 2

Number of species of opisthobranch molluscs known or inferred to have planktotrophic, lecithotrophic or direct development in the tropical eastern Pacific Ocean, compared to the NE Pacific and tropical western Atlantic Oceans.

Region	Mode of development			Sources of data
	Planktotrophic	Lecithotrophic	Direct	
NE Pacific	116	4	6	Goddard (2004, 2005) Krug et al. (2007)
E tropical Pacific	100	4	0	Harris (1975), Bandel (1976), Clark & Goetzfried (1978), Switzer-Dunlap (1978), Schmekel & Portmann (1982), Gonsalves-Jackson (2004), Goddard (2004), present study
W tropical Atlantic	71	24	17	Bandel (1976), Clark & Goetzfried (1978), Eyster (1980, 1981), Clark & Jensen (1981), DeFreese & Clark (1983), Carroll & Kempf (1990), Ortea (2001), Gonsalves-Jackson (2004), Pierce et al. (2006), Valdés et al. 2006

Table 3

Number of species of opisthobranchs from the tropical eastern Pacific and tropical western Atlantic Oceans known or inferred to have planktotrophic or non-planktotrophic (= lecithotrophic and direct) development, by taxonomic family. Based on sources listed in Table 2; taxonomic classification according to Behrens & Hermosillo (2005) and Valdés et al. (2006). A blank space means that no representatives of that family are known from that ocean.

Family	Tropical eastern Pacific		Tropical western Atlantic	
	Planktotrophic	Non-planktotrophic	Planktotrophic	Non-planktotrophic
Aegiretidae	1	0	0	0
Aeolidiidae	6	1	3	2
Aglajidae	2	0	3	0
Aplustridae			2	0
Aplysiidae	10	0	7	1
Arminiidae	1	0	1	1
Boselliidae			1	0
Bullidae	0	0	1	0
Caliphyllidae	1	0	2	1
Chromodorididae	9	0	8	5
Conualevidae	1	0		
Corambidae	1	0	1	0
Cylichnidae	2	0	0	0
Dendrodorididae	3	0	2	4
Dorididae	18	0	8	4
Dotoidae	5	0	4	4
Eubranchidae	3	0	0	0
Facelinidae	5	1	3	3
Flabellinidae	4	0	1	0
Goniodorididae	2	0	3	0
Haminoeidae	2	0	3	1
Hancockiidae	2	0	0	0
Hermaeidae	0	0	2	0
Hexabranchidae			0	1
Limapontiidae	1	0	4	2
Lomanotidae	1	1	0	1
Oxynoidae	1	0	2	1
Placobranchidae	3	0	3	7
Pleurobranchidae	4	0	4	2
Polyceridae	4	0	2	0
Tergipedidae	2	1	0	1
Tritoniidae	3	0	1	0
Tylodinidae	1	0	0	0
Zephyrinidae	2	0	0	0
Total no. of species	100	4	71	41

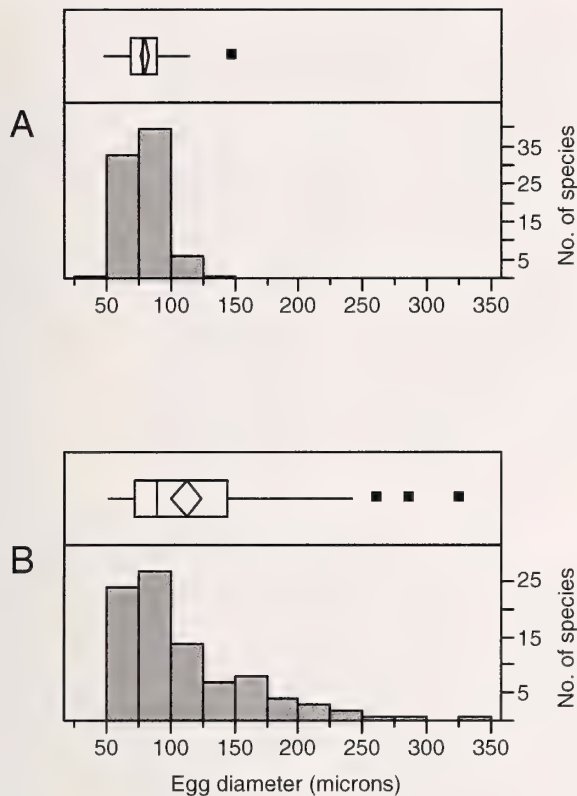


Figure 3. Egg size distributions, with box plots, for Opisthobranchia from the E Pacific ($n = 81$ species) (A) and the W Atlantic ($n = 92$ species) (B). The vertical line in the box plots indicates the sample median, and the diamond indicates the sample mean and 95% confidence intervals. The egg size distribution for the E Pacific is based in part on the upper size limits presented for some species in Table 1. The actual egg sizes for these species are slightly smaller (see heading for Table 1).

the E Pacific, is reflected in the strong skew toward larger egg sizes in the former (Figure 3).

DISCUSSION

Planktotrophy is the dominant mode of development in opisthobranchs from the E Pacific, as in the NE Pacific. Differences in sea surface temperatures aside, both regions have productive waters seemingly conducive for larval feeding and growth. Seasonal, wind-induced, coastal upwelling and the slow-moving, nutrient-rich, California current fuel primary production in the NE Pacific (Bernal & McGowan, 1981; Chelton et al., 1982; Bakun, 1990; Mann & Lazier, 1991), while three types of upwelling (wind-induced coastal, equatorial, and that associated with the cyclonic gyre known as the Costa Rica dome) fuels production in the E Pacific (Wyrtki, 1964; McCreary et al., 1989; Mann & Lazier, 1991; Fielder, 1992). Larval food supplies in both regions are therefore probably rarely limiting, contrib-

uting to the evolutionary maintenance of small egg sizes and planktotrophy in taxa not historically constrained to non-feeding modes of development.

The lack of directly developing opisthobranchs in the E Pacific stands in contrast to the NE Pacific, where it has so far been documented in 6 species (Table 2). However, development has been examined in less than half of the total number of species of opisthobranchs known from the E Pacific (see Camacho et al., 2005; Hermosillo et al., 2006), and sampling in the E Pacific has been biased toward outer coast habitats and, in our study, the winter season. Additional sampling, including in estuarine habitats and during the summer (when a different complement of warmer water species may be present), may therefore be needed to determine if the observed difference in the frequency of this mode of development is significant. Although direct development is not yet known for any opisthobranch from the E Pacific, we suspect that *Chromodoris* sp. 1 of Hermosillo et al. (2006) may hatch as juveniles, based on its small adult size (10 mm) and a known geographic distribution limited to the Revillagigedo Islands, a small volcanic archipelago located 720 km west of mainland Mexico.

Eight of the species whose development we examined in this study were also identified and studied by Gonsalves-Jackson (2004) in Panama. In all cases our size measurements of eggs and embryos corresponded closely with her measurements of egg size, and our observations and measurements of hatching larvae were consistent with her sketches of embryos, only some of which depicted embryos near hatching (Gonsalves-Jackson did not provide measurements of shell size at hatching for any of the species she examined). The largest discrepancy in egg size was for the aeolid *Flabellina marcusorum*. Although we recorded its early embryos as being 73 μm in largest diameter (indicating a slightly smaller egg diameter), and Gonsalves-Jackson (2004) reported a mean egg diameter of 81.5 μm , this difference is within normal intra-specific variation, especially between different populations (e.g., Goddard, 1984, 2004; Todd et al., 2001).

Planktotrophy was significantly more prevalent in opisthobranchs from the E Pacific than in the W Atlantic, consistent with patterns in egg size and (or) mode of development documented by other workers for prosobranch gastropods, bivalve molluscs, alpheid crustaceans, bryozoans, echinoid echinoderms and reef-forming corals across the Isthmus of Panama (Lessios, 1990; Jackson & Herrera, 1999; Marko & Moran, 2002; Wehrtmann & Albornoz, 2002; Fortunato, 2004; Moran, 2004). Most of these studies intentionally compared life history traits in sister species thought to have diverged as a result of the rise of the Isthmus of Panama, thereby ruling out phylogenetic constraints as the sole determinant of the observed

geographic patterns in developmental mode. Larger egg-sizes and non-feeding modes of development are therefore thought to have evolved in these taxa as a result of environmental factors, namely the drop in productivity of surface waters in the Caribbean Sea and W Atlantic following the rise of the Isthmus of Panama (Bishop & Marra, 1984; Coates & Obando, 1996; Collins, 1996; Allmon, 2001). In this environment, larger eggs (with their greater yolk reserves) might be expected as one mechanism for offsetting the mortality caused directly or indirectly by lower ocean productivity and a poor larval feeding environment (e.g., Vance, 1973; Lessios, 1990). However, evidence presented by Moran (2004) for planktotrophic arcid bivalves, suggests that selection for reduced egg sizes in the E Pacific (in response to increased productivity following the rise of the Isthmus) may have been more important in shaping patterns of egg size across the Isthmus in that taxon. Moran (2004) also rightly notes that differential extinction of species with large eggs in the E Pacific and species with small eggs in the W Atlantic following the rise of the Isthmus might also be important in explaining recent egg size patterns.

Environmental considerations aside, phylogenetic constraints do not appear to be important in explaining the difference in mode of development observed in opisthobranchs across the Isthmus of Panama. Planktotrophy is known from nearly all of the 17 families with non-planktotrophic representatives in the W Atlantic and dominates the 16 of those same families that also occur in the E Pacific (Table 3). Given its widespread distribution among even higher taxonomic levels of opisthobranchs in the W Atlantic, non-planktotrophic development appears to have evolved independently in numerous lineages of opisthobranchs in this region.

The differences in ocean productivity and other environmental factors mentioned above apply on even broader geographic scales, and appear to be reflected in ocean basin-wide patterns of egg size and developmental mode in shallow water nudibranchs, the most species rich group of opisthobranchs (Goddard 1992, in preparation). In particular, data we have presented here support the hypothesis that eastern ocean regions, with their widespread upwelling, productive waters, and slow boundary currents (e.g., Mann & Lazier, 1991), will tend to maintain a higher frequency of planktotrophic development compared to western ocean regions, which have less productive waters at mid to lower latitudes and faster boundary currents, which might increase the risk of advection of larvae away from favorable settlement sites.

Notes on individual species

Lomanotus sp. 1 hatched as small, transparent, planktotrophic larvae with a coiled, type 1 shell

117 μ m long (Table 1). Because shell type is family-specific (Thompson, 1976; Goddard, 2004), the statement, without measurements, by Clark & Goetzfried (1976) that *L. vermiformis* (as *L. stauberi*) has an inflated, type 2 shell requires confirmation, especially given conflicting reports of shell type in the family. Thompson (1961), relying on Pruvot-Fol's (1954, fig. 142g) illustration of a coiled larval shell of *L. genei* Vérany 1846 from Europe, listed this species as having a type 1 shell. However, Thompson & Brown (1984) characterized the family Lomanotidae as having a type 2 shell, presumably based on Clark & Goetzfried's (1976) report for *L. vermiformis*.

Tylodina fungina Gabb 1865

The egg ribbons of *Tylodina fungina* were observed on the surface of its yellow, keratose sponge prey, identified in Bakus & Abbott (1980) as *Aplysina fistularis* (Pallas 1766) (= *Verongia thiona* de Laubenfels 1930). The egg masses were laid flat, often in overlapping, convoluted layers attached primarily to spongin fibers exposed by the grazing activity of adults (Figure 4A & B). The egg ribbons were similar in appearance to those of *T. perversa* (Gmelin 1791) and *T. corticalis* Tate 1889 known from E Australia and the Mediterranean Sea, respectively (Thompson, 1970; image in Poddubetskaia, 2002). The ribbons, though thin, were stiffer than those of most other opisthobranchs (personal observations), and appeared to be reinforced by transverse internal walls (Figure 4B). Egg masses laid on the sponge accumulated minute, golden brown, refractile bodies 1 to 5 μ m in greatest dimension (Figure 4C & D, compare to 4B). These bodies were likely unicellular cyanobacteria known to be associated with the surface layers of species of *Aplysina* (Maldonado & Young, 1998; Friedrich et al., 1999; Becerro et al., 2003; Usher et al., 2004). They did not occur inside the egg capsules of *T. fungina*, and appeared to accumulate in surface folds and furrows (Figure 4C & D). The refractile bodies gave the egg masses an opaque, pale yellow to pale orange-brown appearance and were often dense enough to obscure views of the embryos. In 70% ethanol the egg masses, like the adult slugs, turned deep purple, indicating the presence of uranidine, a pigment sequestered by species of *Tylodina* from their sponge prey (Teeyapant et al., 1993).

Near hatching, the embryos fit very tightly within their egg capsules, and the egg masses did not appear to break down as quickly as observed in more gelatinous opisthobranch egg masses. Hatching larvae lacked both eyespots and propodium, but had a compact, lipid-rich viscera, a distinctive, burgundy-colored mantle organ, and an operculum (Figure 4E). Their type 1 shells averaged 126 μ m in length (Table 1) and consisted of

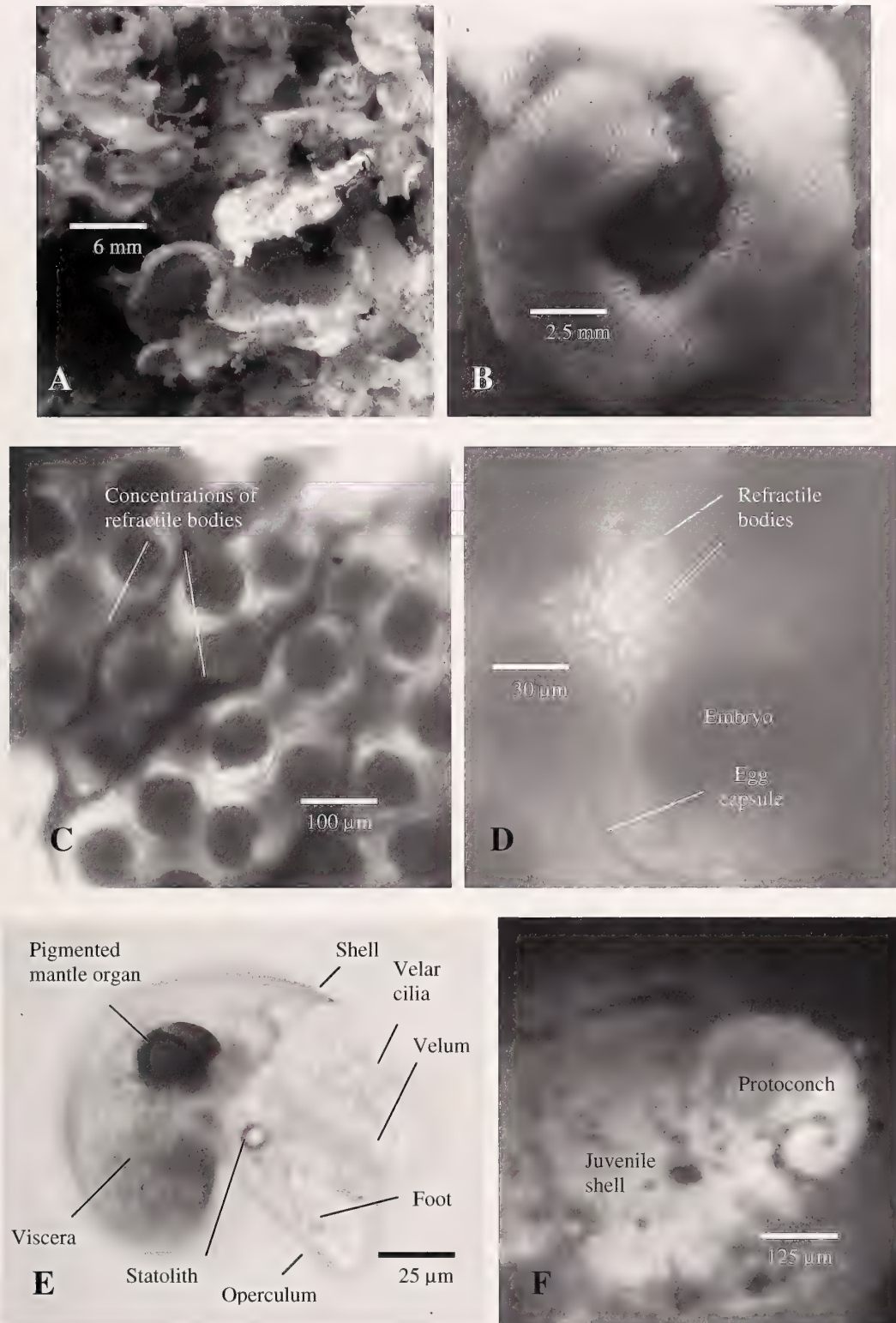


Figure 4. *Tylodina fungina*. A. Egg ribbons laid on spongin fibers and remains of prey sponge, *Aplysina fistularis*. B. Egg ribbon laid on the dorsal surface of the shell of another *Tylodina fungina*. Note the relative transparency of this ribbon compared to those laid on *A. fistularis*. C. Piece of egg mass removed from its sponge substratum, showing concentrations of minute refractile bodies on surface. D. Higher magnification view of minute refractile bodies on surface of egg mass. E. Newly hatched veliger larva, right lateral view. F. Apex of an adult shell (21.3 mm long), showing the protoconch (= embryonic and larval shell), left lateral view, and juvenile shell. Specimen from Bird Rock, La Jolla, California, 12 December 2004.

about two-thirds of a whorl. As observed in pleuro-branches, but not most other hatching planktotrophic opisthobranchs (Gibson, 2003), the mantle was not folded over the edge of the shell. We did not observe vigorous swimming by the newly hatched larvae.

The protoconch of an adult *Tylodina fungina* collected by the senior author at La Jolla, California measured 352 μm in length and consisted of about 1.5 whorls (Figure 4F), indicating that the larvae of this species grow significantly in the plankton. Erosion of the outer layer of the protoconch was evident, but there did not appear to be any demarcation between the embryonic and larval shell (Figure 4F).

Umbraculum umbraculum (Lightfoot 1786) is the only other umbraculoid opisthobranch whose hatching larvae have been described. Like *Tylodina fungina*, the larvae of this species also hatch with coiled shell, a pigmented mantle organ, and an operculum (Ostergaard, 1950; Hartley, 1964). The egg masses, embryo size, and protoconch of *T. perversa* from the Mediterranean Sea appear very similar to those of *T. fungina* (Valdés & Lozouet, 2000; Poddubetskaia, 2002). *Tylodina corticalis* from eastern Australia lays egg masses similar to those laid by *T. fungina*, but with eggs 98 μm in diameter (Thompson, 1970) may have lecithotrophic development.

The small size of the hatching larvae, their lack of both eyespots and propodium, and the size of the protoconch on the adult shell, all indicate that the larvae of *Tylodina fungina* are planktotrophic. However, the viscera developed in a compact arrangement reminiscent of lecithotrophic larvae, and the newly hatched larvae did not appear to be strong swimmers. It would be interesting to know if recently hatched larvae remain in the vicinity of the parental egg masses and consume the microbes associated with the egg masses and underlying sponge. Variation in such behavior might explain the affinity of some adult *Tylodina* for cyanobacteria associated with *Aplysina* (Becerro et al., 2003).

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Three New Buccinid Species (Gastropoda: Neogastropoda) from Chilean Deep-Water, Including One from a Methane Seep

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Abstract. Three deep water species from off the Chilean coast are described as new. *Aeneator prognaviter* sp. nov. (off Antofagasta) is compared with *A. loisae* Rehder, 1971 and *A. castillai* McLean & Andrade, 1982. The peculiar *Aeneator portentosus* sp. nov. (off Coquimbo) has the generic placement based on conchological characteristics and is compared with *Americominella duartei* Klappenbach & Ureta, 1972. *Kryptos explorator* sp. nov. (off Concepción) is compared with *K. koehleri* (Locard, 1896), the generic placement based on conchological characteristics (protoconch and slightly broader peripheral spiral interspace) and radular morphology. *Kryptos explorator* sp. nov. has been collected at a recently discovered methane seep area off Concepción (~36°S), but its degree of association to seep fauna is still uncertain.

Key Words: Gastropoda, Buccinidae, *Aeneator*, *Kryptos*, new taxa, methane-seeps, bio-diversity, East Pacific, Chile.

INTRODUCTION

The coastal zone off north to south-central Chile, strongly influenced by wind-driven upwelling, is one of the areas with the highest known primary production rates worldwide (Daneri et al., 2000). Consequently this area of the south-eastern Pacific Ocean harbours a vast pelagic and benthic biomass. However, in spite that the benthic fauna has been proven to be rich in endemic species, of which many are still undescribed or unknown, its scarce knowledge still precludes researchers have an accurate assessment of the diversity along the Chilean margin.

The existing literature on benthic communities along the continental margin off north to south-central Chile is restricted mostly to the shelf and upper slope (e.g., Gallardo, 1963; Brattström & Johanssen, 1983). Except for the general results of the R/V Anton Bruun cruise in the Southern Pacific (Garth & Haig, 1971; Menzies et al., 1973), the Russian Expeditions (Mironov & Rudjakov, 1990, and references therein) and general studies of the archibenthic fauna (Andrade, 1986, 1987), there are no detailed studies on bathyal benthic communities.

Regarding mollusks, the offshore continental slope and the deep ocean floor were also largely underestimated in the past, if not miserably ignored by collectors

and malacologists. Today we know that the Chilean coastline and adjacent continental slope harbors many species of molluscs. The result of continuous research conducted by scientific expeditions (from the Lund University Chile Expedition in 1948–1949 to the PUCK-156 expedition in 2001, to mention a few), by local trawlers (McLean & Andrade, 1982) and from shrimpers of the former Soviet Union (Fraussen & Hadorn, 2000; Poupin, 2003), have produced noteworthy contributions. Most recently, the existence of methane seepage and associated chemosynthetic communities in the bathyal zone off central Chile (Concepción Methane Seep area or CMSA, Sellanes & Krylova, 2005) has been reported, and sampling has brought to light many new bathyal species. Some of the associated chemosymbiotic bivalves found (e.g., *Calypptogena*, *Lucinoma* and *Thyasira* have recently been described (Holmes et al., 2005; Oliver & Sellanes, 2005; Sellanes & Krylova, 2005). New species of gastropods have been named (e.g., *Trophon conceptionensis*, Houart and Sellanes, 2006; *Otukaia crustulum* and *Margarites huloti*, Vilvens and Sellanes, 2006). In the present article we add to this list a new buccinid species from this seep area as well as two new species from the north to central Chile margin.

The goal of the present paper is thus to contribute to

the knowledge of the family Buccinidae from north to south-central Chile and to continue the effort of describing the malacofauna of the CMSA

ABBREVIATIONS

AGT	Agassiz trawl
CMSA	Concepción Methane Seep Area
JS	collection of Javier Sellanes, Chile
KF	collection of Koen Fraussen, Belgium
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHNCL	Museo Nacional de Historia Natural, Santiago, Chile.
lv	live collected specimen
dd	empty shell

SYSTEMATICS

Class: Gastropoda Cuvier, 1797

Order: Neogastropoda Wenz, 1938

Subfamily: Buccinoidea Rafinesque, 1815

Family: **Buccinidae** Rafinesque, 1815

Genus: *Aeneator* Finlay, 1927:414.

Type species. *Verconella marshalli* Murdoch, 1924 (by original designation). Fossil, Tertiary, New Zealand.

Definition. The genus *Aeneator* is present mainly in the West Pacific, with the geographical center situated around New Zealand, and with an important fauna off southern West America. For an overview of the genus off New Zealand, we refer to Powell (1979:201–203).

Here we follow the opinion of McLean & Andrade (1982:12–13) and use *Aeneator* in a broad sense, without subgeneric splitting for the Chilean species.

Three species were previously known from Chilean waters: *Aeneator fontainei* (d'Orbigny, 1839), *Aeneator (Ellicea) loisae* Rehder, 1971 and *Aeneator castillai* McLean & Andrade, 1982.

Aeneator prognaviter new species

(Figures 1–2, 12–15)

Type material. Holotype (MNHNCL-5863) (32.2 mm), Chile, off Antofagasta 22°51'99 S, 70°29'40 W, in 318 m, lv.

Paratype 1 (KF-5178) (26.0 mm), same locality as holotype, lv; paratype 2 (MNHNCL-5864) (29.2 mm), same locality as holotype, dd.

Type locality. Chile, north of Antofagasta, Chilean upper continental slope, in 318 m.

Range and habitat. Only known from the type material.

Description. Shell small for genus (up to 32.2 mm), thick, solid, snow white. Shape broad with moderately high spire, whorls convex, slightly angulate, suture deep.

Upper whorls and protoconch eroded, about 4 1/2 teleoconch whorls remaining of which only 3 1/2 with sculpture intact.

Spire whorls with 8 or 9 broad spiral cords with rather sharp top, interspaces broad, of equal size. Body whorl with 20–24 spiral cords, occasionally alternating fine and sharp.

Spire whorls with 17–19 pronounced, slightly curved axial ribs, interspaces deep, broad. Body whorl with 22 such axial cords, gradually becoming weaker towards outer lip.

Aperture oval, columella smooth, slightly curved, outer lip thin, simple, edge sharp. Siphonal canal short, broad, open.

Operculum small, thin, transparent, yellowish brown, elongate, nucleus terminal, tip sharp.

Comparison. *Aeneator prognaviter* sp. nov. is characterized by broad shape with angular whorls, curved axial ribs and short siphonal canal.

Aeneator loisae Rehder, 1971 and *A. castillai* McLean & Andrade, 1982 both differ in having a higher number of spiral cords in combination with a lower number of axial ribs, spiral cords with a convex top (instead of sharp) and usually a higher number of secondary spiral cords (instead of alternating fine and strong), axial ribs which are straight (instead of bent and curved) and a larger adult size.

Aeneator recens (Dell, 1951) from New Zealand is somewhat similar in shape, axial sculpture, size and colour but differs by having narrower spiral cords with broader interspaces, a longer siphonal canal and a curved operculum.

Etymology. *Aeneator prognaviter* sp. nov. is named after the Latin expression “prognaviter,” meaning “clearly” and “brief and to the point” or “short but sweet” (as adverbium), or meaning “also” (as substantivum), which refers to the shell which is clearly an *Aeneator*. It also refers to the small size (short or brief) but still an *Aeneator* (to the point).

Aeneator portentosus new species

(Figures 3–4, 7–11)

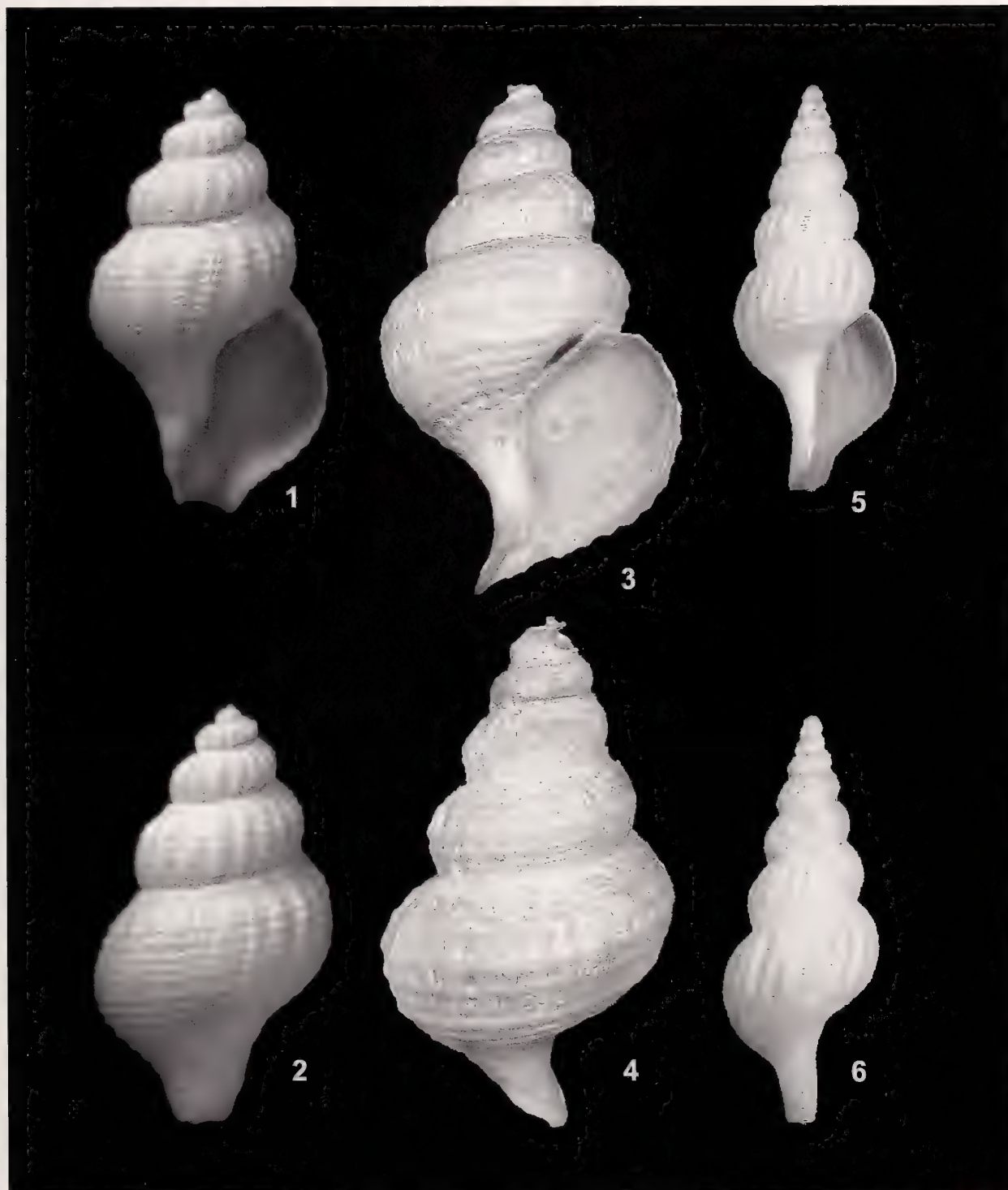
Type material. Holotype (MNHNCL-5865) (44.9 mm, siphonal canal broken), Chile, continental slope off Iquique, 21°19' S, 70°26' W, in 605 m, dd.

Paratype (KF-0338) (45.5 mm), off Coquimbo, 800 m deep, trawled by fisherman.

Type locality. Chile, off Iquique, 21°19' S, 70°26' W, in 605 m.

Range and habitat. Only known from the type material.

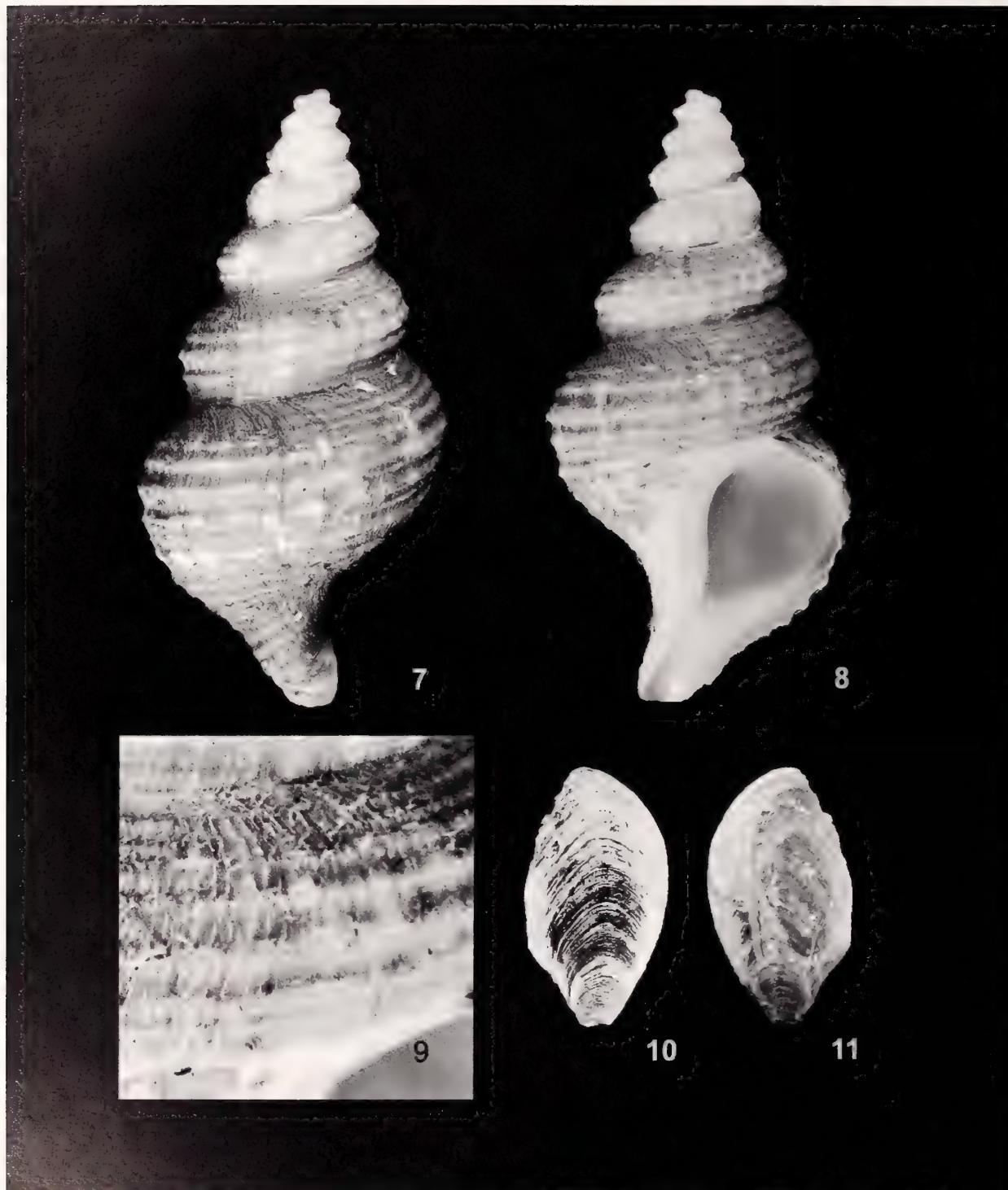
Description. Shell medium (up to 45.5 mm), thin but solid, snow white. Shape elongate with high spire. Whorls angulate, upper spire whorls rather pagodoid. Spiral sculpture dominant.



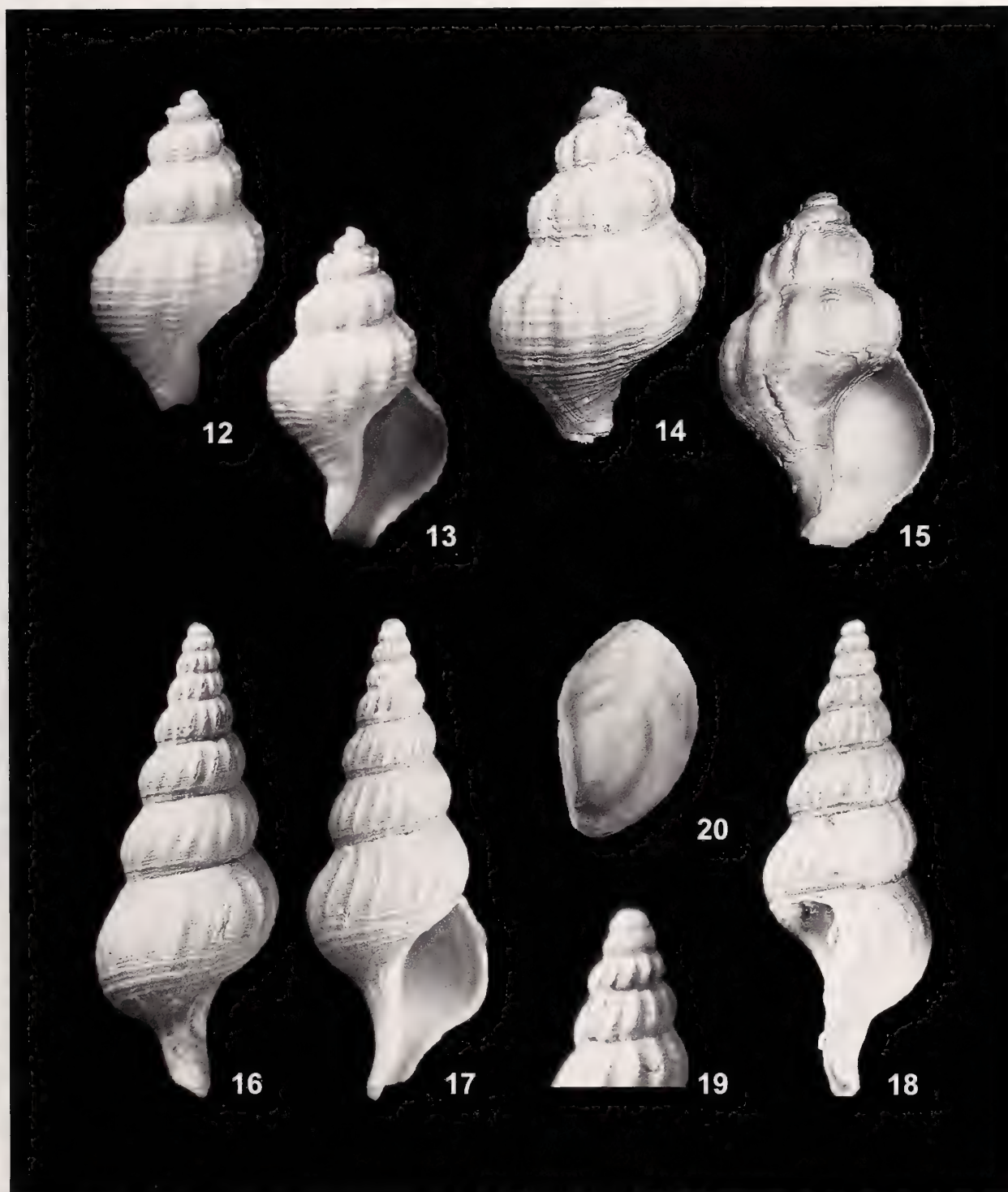
Figures 1–2. *Aeneator prognaviter* sp. nov., holotype, 32.2 mm, Chile, off Antofagasta 22°51'99 S, 70°29'40 W, 318 m, MNHNCL-5863.

Figures 3–4. *Aeneator portentosus* sp. nov., holotype, 44.9 mm, Chile, off Iquique 21°19S, 70°26W, 605 m., MNHNCL-5865.

Figures 5–6. *Kryptos explorator* sp. nov., holotype, 29.6 mm, Chile, northwest of the Bay of Concepción 36°20'97 S, 73°44'86 W, 850 m, MNHNCL-5866.



Figures 7–11. *Aeneator portentosus* sp. nov., paratype, 45.5 mm, Chile, off Coquimbo, 800 m, KF-0338.



Figures 12–13. *Aeneator prograviter* sp. nov., paratype 1, 26.0 mm, Chile, off Antofagasta 22°51'99 S, 70°29'40 W, 318 m, KF-5178.

Figures 14–15. *Aeneator prograviter* sp. nov., paratype 2, 29.2 mm, Chile, off Antofagasta 22°51'99 S, 70°29'40 W, 318 m, MNHNCL-5864.

Figures 16–20. *Kryptos explorator* sp. nov., 16–19. paratype 3, 28.9 mm, Chile, northwest of the Bay of Concepción 36°22'68 S, 73°42'46 W, 708–709 m, KF-5180. 20. operculum of holotype, 6.6 mm.

Upper whorls and protoconch eroded.

All whorls with 6 or 7 sharp spiral cords, subsutural cord weak, gradually stronger along subsutural slope, pronounced on periphery, forming a carina. Interspacing broad, bottom weakly concave. Body whorl with about 20 spiral cords, 3 or 4 weak ones on subsutural slope, 2 or 3 strong ones on periphery, gradually becoming slightly weaker towards siphonal canal.

Upper spire whorls eroded but numerous fine axial ribs still traceable, more pronounced on periphery and on top of spiral cords. Axial ribs gradually weaker towards penultimate whorl. Body whorl smooth. All whorls covered by fine incremental lines.

Aperture round, columella smooth, slightly curved, outer lip thin, simple, edge sharp. Siphonal canal moderately short, broad, open, slightly bent.

Periostracum (paratype 1) thick, ornamented with a dense sculpture of fine, sharp axial lamellae, running from suture to suture, forming sharp spines or hairs on transition with spiral sculpture.

Operculum small, thin, corneous, dark brown, elongate, nucleus terminal, tip sharp.

Comparison. *Aeneator portentosus* sp. nov. is characterized by the rather pagodoid shape, the pronounced spiral sculpture and the densely sculptured periostracum.

The generic placement is based on conchological characteristics and on the shape of the operculum.

All *Aeneator* species known from Chile differ by having more convex whorls, a slightly longer siphonal canal, narrower spiral interspaces and a smoother periostracum.

Etymology. *Aeneator portentosus* sp. nov. is derived from the Latin expression *portentosus* (adjective), meaning "wonderful," which refers to the graceful shape and excellent sculpture.

Genus *Kryptos* Jeffreys in Dautzenberg & Fischer, 1896

Type species. *Kryptos elegans* Jeffreys in Dautzenberg & Fischer, 1896 (type locality: "bathyal, W. of Spain" designated by Bouchet & Warén, 1985:196), by monotypy, a junior synonym of *Pleurotomella koehleri* Locard, 1896.

Transferred to Buccinidae by Bouchet & Warén (1985:195), based on morphology of the radula.

Range, until the present paper, restricted to the Atlantic Ocean, the two known species being *K. koehleri* (Locard, 1896) (= *Kryptos elegans* Jeffreys in Dautzenberg & Fischer, 1896; *Pleurotomella atlantica* Locard, 1897 and *Pleurotomella demulcata* Locard, 1897) from the N. E. Atlantic and *K. tholoides* (Watson, 1882) from the S. W. Atlantic (off Brazil).

Remarks. *Kryptos* is characterized by a multispiral, rather big protoconch with a slightly flattened tip,

sculptured towards transition to the teleoconch (Figure 28), a smooth, narrow subsutural band, a slightly broader interspaces on the periphery, carinated whorls (type species) or sculptured with some sharp keels (*K. tholoides*). Bouchet & Warén (1985:196) noted that *K. koehleri* lack eyes.

Americominella Klappenbach & Ureta, 1972 (type species: *Americominella duartei* Klappenbach & Ureta, 1972) from the Patagonian continental shelf is similar in protoconch morphology and sculpture but differs by the radula, which has a tricuspid central tooth with broad base.

Kapala Ponder, 1982 (type species: *Kapala kengrahami* Ponder, 1982) from Australia has a radula with an identical central tooth but which differs by having the lateral teeth with 1 large outer cusp and more than 5 small inner cusps.

Antarctoneptunea Dell, 1972 (type species: *Fusitriton aurora* Hedley, 1916) is similar in shape but differs in having a large papilliform protoconch (similar to *Aeneator*) and a radula with tricuspid central tooth.

The new species described below is tentatively placed in *Kryptos* based on similarities in radula, protoconch and spiral sculpture.

Kryptos explorator new species

(Figures 5–6, 16–25)

Type material. Holotype (MNHNCL-5866) (29.6 mm), south-central Chile, R/V Vidal Gormáz (SeepOx cruise, AGT 6–7, 09/02/2006), CMSA, northwest of the Bay of Concepción 36°20'97 S, 73°44'86 W, 850 m, lv.

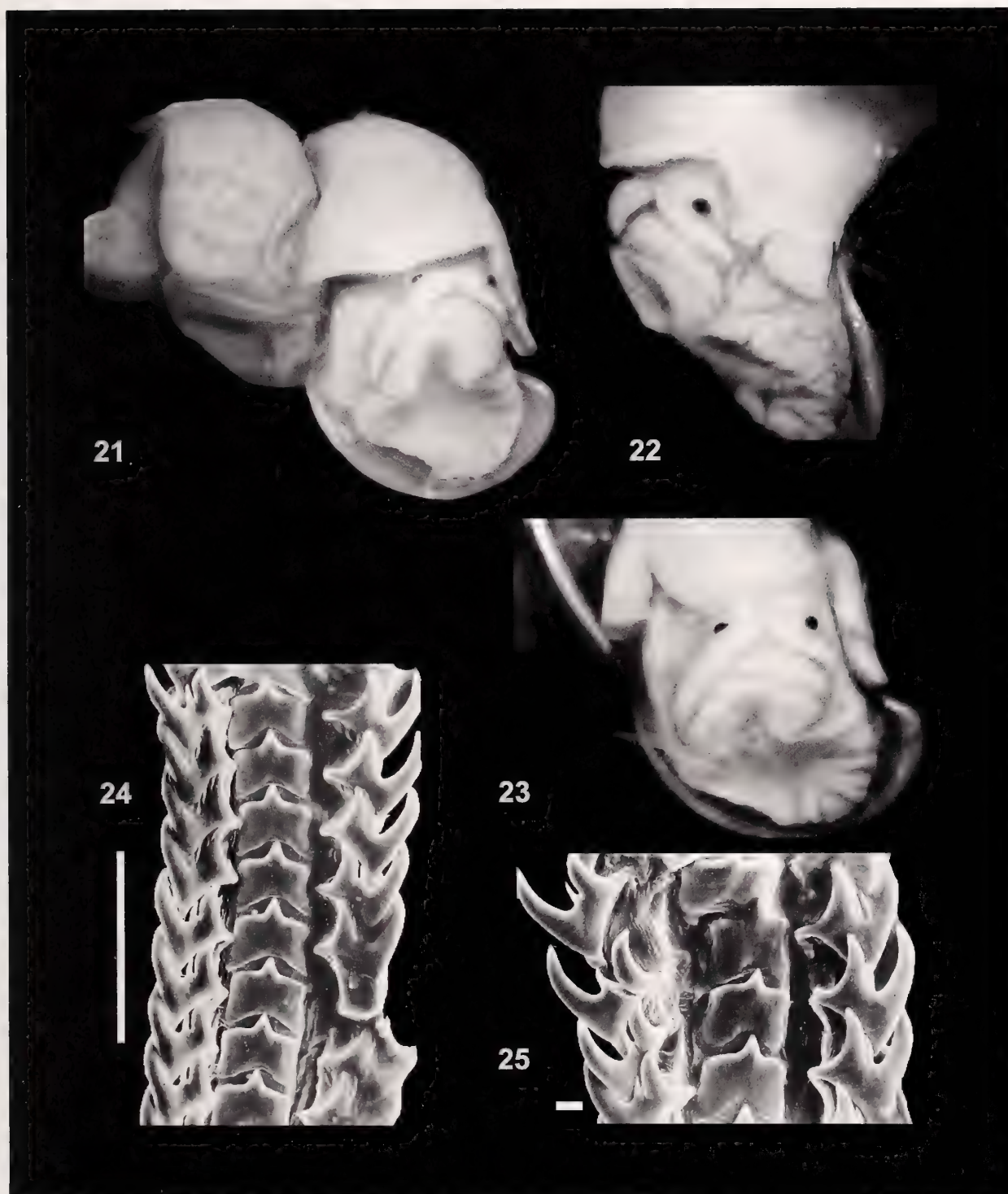
Paratype 1 (MNHNCL-5867) (29.4 mm), same locality as holotype, lv; paratype 2 (MNHNCL-5868) (29.3 mm), same locality as holotype, lv; paratypes 3 & 4 (KF-5180–5181) south-central Chile, R/V Vidal Gormáz (VG-04 Cruise, AGT 10, 10/14/2004), CMSA, northwest of the Bay of Concepción, 36°22'68 S, 73°42'46 W, 708–709 m; paratype 5 (MNHN-9961) same locality of paratypes 3 & 4.

Type locality. South-central Chile, R/V Vidal Gormáz (SeepOx Cruise, AGT 6–7, 09/02/2006), CMSA, northwest of the Bay of Concepción, 36°20'97 S, 73°44'86 W, 850 m.

Range and habitat. Only known from the type material. All the specimens of *K. explorator* sp. nov., so far collected have been associated with fauna typical of methane seeps (vesicomysid, solemyid, lucinid and thyasirid bivalves). However, the scarce knowledge of the bathyal SE Pacific malacofauna still prevents us from establishing if this new species lives in an obligate association with seep environments.

Description. Shell small (up to 29.6 mm), thin but solid, semi-transparent, white. Shape fusiform with slender spire.

Protoconch multispiral, consisting of about 2 1/4



Figures 21–25. *Kryptos explorator* sp. nov., holotype, Chile, northwest of the Bay of Concepción 36°20'97 S, 73°44'86 W, 850 m, MNHNCL-5866. 21. frontal view of removed animal. 22. left side view. 23. close up of the head showing the remarkable eyes. 24. radula, scalebar: 100 micrometer. 25. radula, scalebar: 10 micrometer.

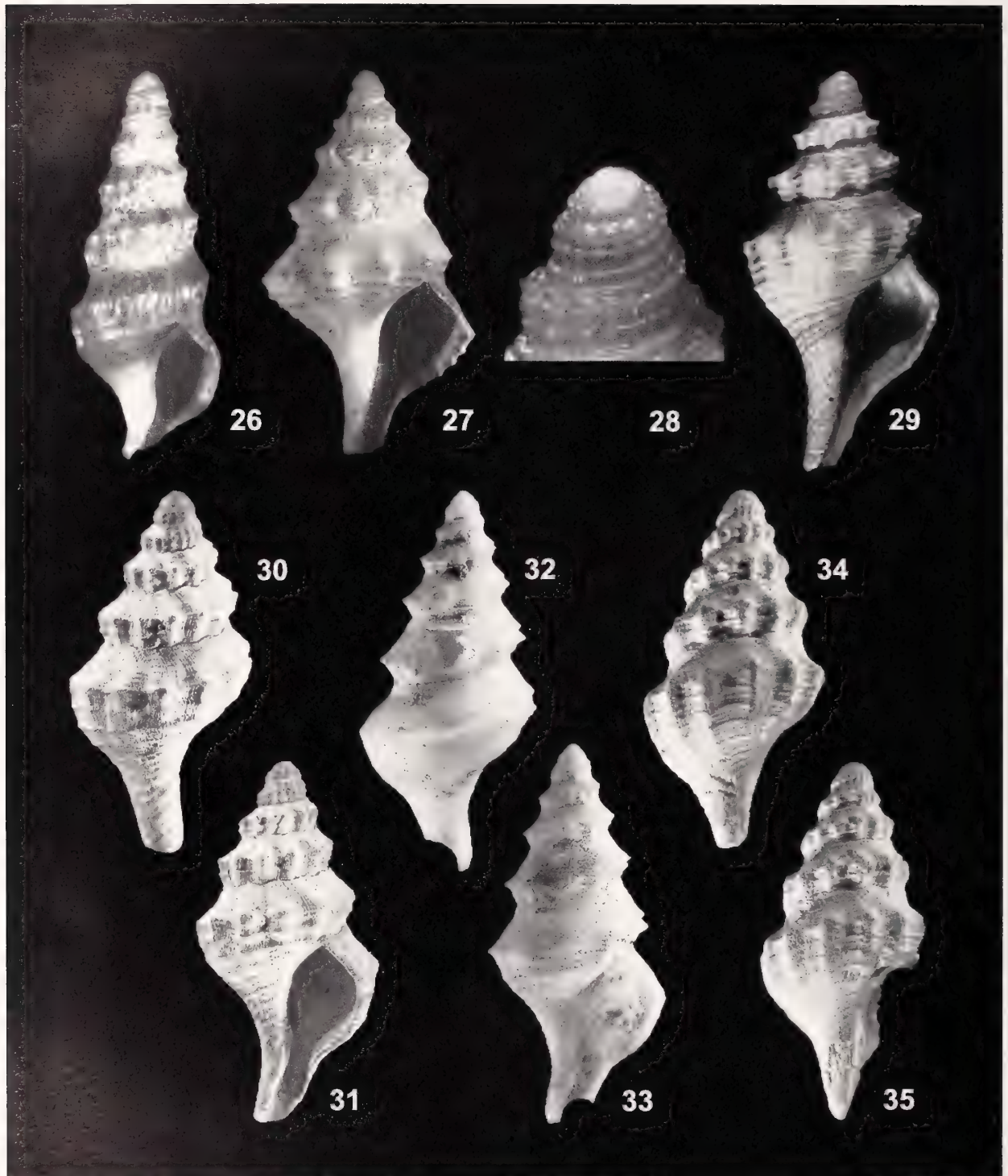


Figure 26. *Krypthos tholoides* (Watson, 1882), holotype, 16.1 mm, BMNH, after Bouchet & Warén, 1986, fig. 96. Figures 27–35. *Kryptos koehleri* Locard, 1896. 27. 21.8 mm, Gulf of Biscay, BIOGAS CP25, 44°05'N, 04°17'W, 1894 m, after Bouchet & Warén, 1985, fig. 511. 28–29. 11.8 mm, off Portugal, after Bouchet & Warén, 1985, fig. 512. 30–31. holotype of *Pleurotomella elegans* Jeffreys in Dautzenberg & Fischer, 1896, 12.0 mm, MNHN-6422. 32–33. holotype of *Pleurotomella atlantica* Locard, 1897, 16.5 mm, MNHN-6647. 34–35. holotype of *Pleurotomella demulcata* Locard, 1897, 13.2 mm, MNHN-6645.

whorls, about 1.6 mm in diameter, tip flattened, last whorl rather big, convex, ornamented with a reticulate sculpture of 7 or 8 fine spiral cords and numerous fine axial lamellae. Sculpture appearing as small holes when slightly eroded (first protoconch whorl). Transition to teleoconch indistinct.

Teleoconch whorls up to 7 in number, convex, adapical part slightly flattened, accentuating a conical shape. Suture distinct.

First whorl with 7 spiral cords, at first smooth and weak, gradually becoming stronger and more convex, with deep interspaces of equal width. Second whorl with 8 sharp, narrow spiral cords, interspaces twice as broad. Spiral cords suddenly broader and weaker, but occasionally still sharp, with variable interspaces, usually narrow. Third whorl with 12 spiral cords of mixed strength. Body whorl adapically rather smooth, with numerous weak or obscure spiral cords; base strongly sculptured with about 9 strong spiral cords. Siphonal canal rather smooth with about 15 weak spiral cords.

First teleoconch whorl with fine axial riblets at beginning, gradually becoming stronger, waving on top of spiral cords, second whorl with pronounced, sharp, narrow axial ribs, slightly weaker near sutures. Second whorl with 13, third whorl with 14 such ribs. Penultimate and body whorl with 17 axial ribs on adapical half of body whorl, base smooth. All whorls covered with fine, slightly curved incremental lines.

Aperture round, columella gently curved, callus thin, smooth. Outer lip thin, sharp, laterally curved according to incremental lines. Siphonal canal narrow, rather short, open.

Operculum corneous, thin, pale brownish, elongate, nucleus terminal, tip sharp.

Periostracum yellowish to pale brown, thin, smooth, well adherent.

Radula (Figures 24–25) typical for genus: central tooth rather rectangular with concave base and 1 short cusp, lateral teeth tricuspid with large outer cusp and small middle cusp.

Animal (Figures 21–23) pale yellowish, with 2 short but broad tentacles and black, rather big eyes.

Comparison. *Kryptos explorator* sp. nov. is characterized by having a fusiform shape, a multispiral, rather big protoconch with a slightly flattened tip and a reticulate sculpture near the transition to teleoconch, a smooth, narrow subsutural interspace between suture and shoulder and slightly broader, smooth interspaces on the periphery.

K. koehleri (Locard, 1896) (Figures 27–35) differs by having a broad shape with strongly angulate whorls and by lacking eyes.

K. tholoides (Watson, 1882) (Figure 26) differs by having 2 strong spiral folds, broader interspaces and a glossy surface.

Etymology. *Kryptos explorator* sp. nov. is named after the Latin expression *explorator* (subst., m) meaning “a scout” or “the one who search out,” which refers to the range (the Pacific, new for the genus and far from the Atlantic) where this new species is found. It also refers to the presence of eyes (to explore the new habitat visually) which are absent in the type species (*K. koehleri*).

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Redescription of the Deep-sea Wood Borer *Neoxylophaga teramachii* Taki & Habe, 1950 and its Assignment to the Genus *Xyloredo* (Bivalvia: Myoida: Pholadoidea) with Comments on Fossil Pholadoidae

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Abstract. Examination of the type specimens of the Japanese wood-borer *Neoxylophaga teramachii* Taki & Habe, 1950 and additional live and dead intact specimens has revealed that the species should be reallocated to the genus *Xyloredo* Turner, 1972, the third genus of Xylophaginae, because it has: 1) a teredo-like calcareous tube, 2) a greatly reduced calcareous mesoplax, and 3) extended inhalant and exhalant siphonal canals, all features typical of *Xyloredo*. *Mesoxylophaga* Habe, 1977, established for *N. teramachii*, is therefore regarded as the junior synonym of *Xyloredo*. Since the present species is extremely rare and its soft parts never studied, a detailed redescription is given for shell, mesoplax, calcareous tube and soft parts. Two unique organs considered to function in self-fertilization, the accessory genital organ and *vesicula seminalis*, are observed for the first time for *Xyloredo*. The associated calcareous tube shows unique microstructure referred to isolated crystal morphotypes. The mineralogy of the calcareous tube consists entirely of aragonite, and the general morphology of the tube is characterized by remarkably strong, regular growth lines in its surface. These features in the calcareous tube provide useful criteria for identification of the trace fossil *Teredolites* in the Mesozoic and Cenozoic.

INTRODUCTION

The Xylophaginae is a subfamily of Pholadidae and, according to Turner (2002), composed of three genera, *Xylophaga* Turton, 1822, *Xylopholas* Turner, 1972a, and *Xyloredo* Turner, 1972b. All species of this subfamily are obligate borers in sunken woods, mostly in deep seas. Knudsen (1961) described 17 species of *Xylophaga* in the collection obtained during the Galathea Deep Sea Expedition from 1950 to 1952. Subsequently, Turner (2002) revised previously reported species and described seven additional new species. Both authors demonstrated that the soft parts, such as siphons, mesoplax and accompanying external morphology (e.g., ‘chimney’ and ‘tube’ seen in their burrows) are important characters for the systematics of this subfamily; shell characters are generally not useful because they share almost homogeneous, simple, spherical, and *Teredo*-like valves. Therefore, detailed examination of intact live animals is indispensable for the systematics of this bivalve group. However, intact live animals are quite difficult to obtain due to their deep-sea occurrence and the fragile nature of the shells.

Japanese authors proposed four subgenera within the genus *Xylophaga* all diagnosed by shell characters alone. These are *Protoxylophaga* Taki & Habe, 1945; *Neoxylophaga* Taki & Habe, 1945; *Metaxylophaga* Taki & Habe, 1945; and *Mesoxylophaga* Habe, 1977. Turner (1969, 2002), Hoagland & Turner (1981), and Hoagland (1983) synonymized all the subgenera with *Xylophaga*. However, such taxonomic treatments need to be confirmed on the basis of detailed examination of soft parts.

Neoxylophaga teramachii Taki & Habe (1950) is a case of such examples. It was described on the basis of specimens from Tosa Bay, Kochi Prefecture in western Japan. Subsequently, Habe (1977) established the monotypic new subgenus *Mesoxylophaga* under the genus *Neoxylophaga* with *N. teramachii* as the type species. Kuroda & Habe (1981) later ranked *Mesoxylophaga* at the genus level, and this taxonomic treatment has been followed by subsequent Japanese authors (e.g., Higo & Goto, 1993; Higo et al., 1999). Okutani (2000) considered *Mesoxylophaga* as a subgenus of *Xylophaga* without any discussion. *N. teramachii* is very rare, and Pailleret et al. (2007: p. 237, fig. 3) documented for the first time since the description by

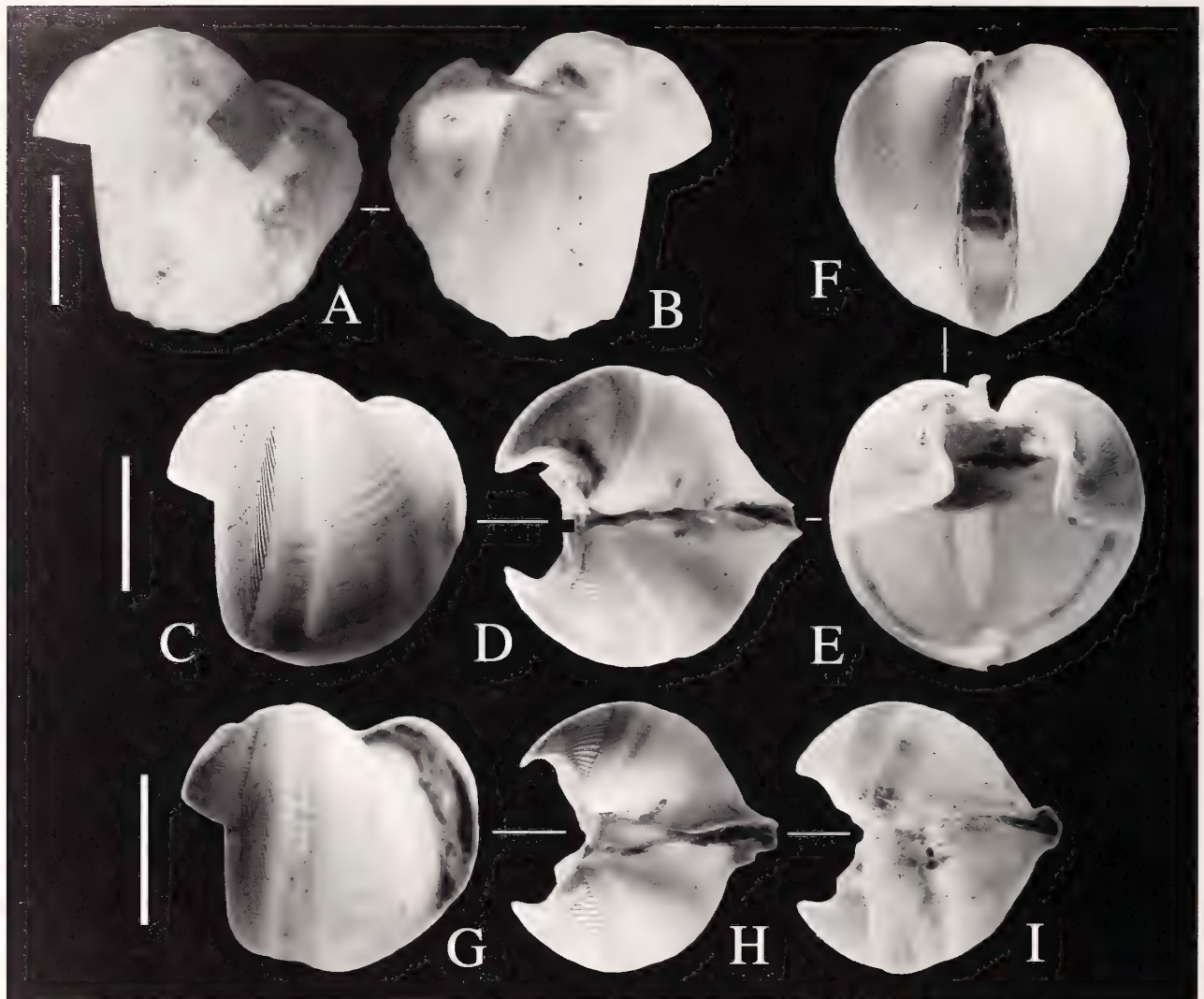


Figure 1. Type specimens of *Xyloredo teramachii* deposited in the Toba Aquarium labeled as TA-7097. A–B. Holotype. C–F. Paratype #1. G–I. Paratype #2. Scale bars = 5 mm.

Taki & Habe (1950) a live animal of this species from a deep-sea bottom off Vanuatu.

This paper reexamines the type specimens of *N. teramachii* deposited in the Toba Aquarium, Toba City, Mie Prefecture, Japan, as well as describes in detail the shell, mesoplax, accompanied calcareous tube, and soft parts of *N. teramachii* on the basis of additional live and dead specimens obtained by the first author from his recent extensive field sampling. We show that this species can be reallocated to *Xyloredo*, another genus of Xylophaginae, and that *Mesoxyllophaga* is a junior synonym of *Xyloredo* instead of a subgenus of *Xylophaga*. In addition, this paper first documents the mineralogy and microstructure of the calcareous tube of the genus *Xyloredo*.

Institutional Abbreviations: NSMT—National Museum of Nature and Science, Tokyo, Japan (formerly National Science Museum, Tokyo); OKCAB—Okayama University, Conservation of Aquatic Biodiversity, Okayama, Japan; TA—Toba Aquarium, Mie, Japan.

MATERIALS AND METHODS

Holotype: Left valve (11.62 mm in height, 12.73 mm in length, TA-7097: Figure 1A–B), possibly taken alive. Taki & Habe (1950) described the present species based on a single conjoined specimen and illustrated it with a freehand figure. The ‘holotype’ deposited in the Toba Aquarium with the registration number TA-7097 consists only of a left valve, although it was ‘conjoined’

in the original description, of which Higo et al. (2001) were aware. Its dimensions do not match well with those given in the original description. However, this 'holotype' specimen matches the figure and retains part of the dried-up posterior adductor muscle within the valve, suggesting that it was originally a conjoined valve. Shell dimensions sometimes differ because of varying measuring methodologies. We therefore regard TA-7097 as the holotype.

Paratypes: Two conjoined shells (Paratype #1, 11.90 mm in height, 11.15 mm in length: Figure 1C–F; Paratype #2, 8.93 mm in height, 9.91 mm in length: Figure 1G–I), possibly taken alive from the type locality. Although Taki & Habe (1950) did not mention paratypes in the original description, two conjoined specimens were labeled and preserved under the registration number of TA-7097, the same as the holotype (Figure 2). The type specimens deposited in the Toba Aquarium are briefly labeled and holotypes and paratypes are distinguished with red and blue labels, respectively (M. Isowa, personal communication). Although the other two specimens are not marked with blue labels, they are regarded as paratypes.

Other material: JAPAN—Five empty shells, one individual with decayed animal and fragments of tubes inside a sunken wood trunk recovered by a commercial trawler at 200 m deep off Tokai, Ibaraki Prefecture, April 29, 2004, *leg.* T. H. (NSMT-Mo76705); 50 empty shells, two live individuals and nine almost intact tubes, inside a sunken wood trunk recovered by a commercial trawler at a depth of 125 m off Tokai, Ibaraki Prefecture, June 3, 2004, *leg.* T. H. (NSMT-Mo76706; OKCAB M15894); 12 empty shells and fragments of tubes, inside a sunken wood trunk recovered by a commercial trawler at a depth of 500 m off Hitachi, Ibaraki Prefecture, March 10, 2007, *leg.* T. H. (NSMT-Mo76707); three empty shells and four tubes, inside a sunken wood trunk, 250–300 m deep off Atsumi Peninsula, Aichi Prefecture, February 1999, *leg.* S. Kimura (NSMT-Mo76708). VANUATU—two intact specimens; BOA0, from a depth of 560–580 m between Malekula and Epi Island, Vanuatu, inside a sunken wood trunk identified either as *Leucaena* or as *Serianthes*, November, 2004, R/V *Alis* (NSMT-Mo73806, 73807) (Pailleret et al., 2007).

Methods: Since the outer morphology of soft body *in situ* provides characters indispensable for systematics, we exposed the animals by breaking the wood with special care, and then observed and photographed the specimens. We used one of two live individuals (originally prepared for molecular analysis with 99% ethanol, following Ueshima, 2002) recovered from off

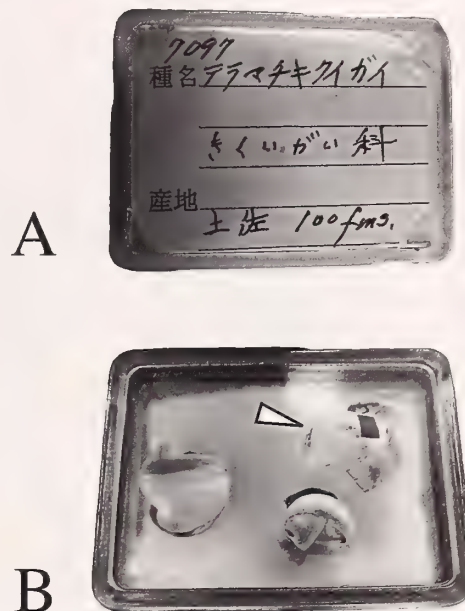


Figure 2. Type specimens of *Xyloredo teramachii* with the attached label in the Toba Aquarium, registered as TA-7097. A. The label. Japanese texts mean Japanese name (teramachikukai-gai = teramachi xylophagain clam), the family (kikai-gai-ka = Xylophagaidae), and the locality (Tosa 100 fms. = Kochi Prefecture, ~100 fathoms deep) from top to bottom, respectively. B. Type specimens. Arrowhead indicates the holotype. Note a boxed seal attaching the holotype.

Tokai, Ibaraki, Japan in June, 2004 for gross anatomy. This material was strongly dehydrated, so that we employed a method improved from Fukuda & Ekawa (1997): (1) the whole animal was immersed in 5% HCl solution for 30 min to rehydrate it sufficiently for dissection, (2) rinsed with tap water for 10 min, and then (3) dissected in 70% ethanol under a binocular microscope. As the dried periostracal sheath was strongly contracted, it was photographed by immersing in 70% ethanol. Scanning electron microscopy (SEM) micrographs were produced on a JOEL-T330A scanning electric microscope after the preparation of material with the standard method: material was cleaned and rinsed with distilled water, hydrated with pure ethanol, dried, mounted on the stages, and then coated with gold. For prodissococonch observation, the shelled structure covering the umbo was removed manually to expose the prodissococonch prior to the preparation. X-ray diffraction analyses were conducted for mineralogical determination of the shell and calcareous tubes. All the specimens used in this study are housed at NSMT (NSMT-Mo 76705–76708).

We followed Purchon (1941) and Turner (2002) for the terminology of anatomical and conchological characters, respectively, except for 'dorsal portion of

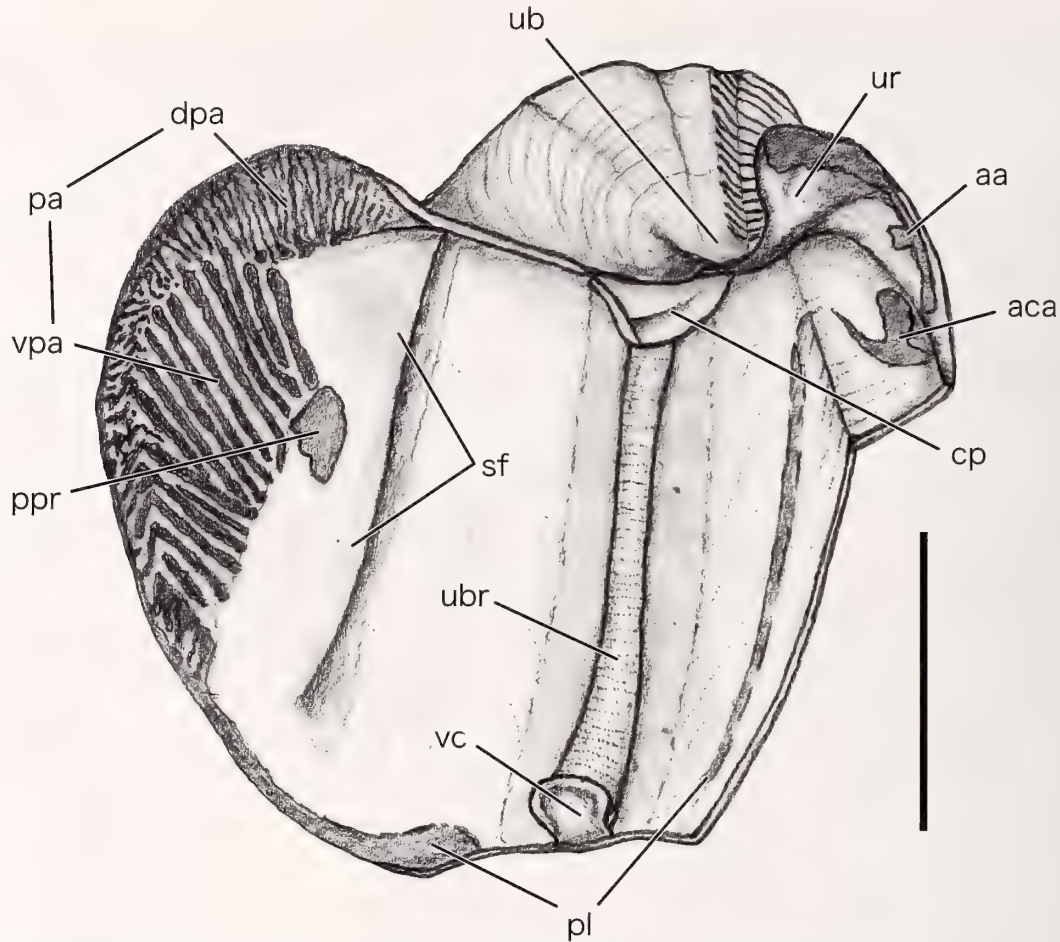


Figure 3. Internal left valve of *Xyloredo teramachii*. Abbreviations: aa = anterior adductor scar, aca = accessory anterior adductor scar, cp = chondrophore, dpa = dorsal portion of posterior adductor scar, pa = posterior adductor scar, pl = pallial line, ppr = posterior pedal retractor scar, sf = shelf, ub = umbo, ubr = umbonal-ventral ridge, ur = umbonal reflection, vc = ventral condyle, vpa = ventral portion of posterior adductor scar. Scale bar = 5 mm.

posterior adductor,' 'ventral portion of posterior adductor' and 'accessory anterior adductor,' which are newly introduced herein.

SYSTEMATICS

Superfamily Pholadoidea Lamarck, 1809

Family Pholadidae Lamarck, 1809

Subfamily Xylophaginae Purchon, 1941

Genus *Xyloredo* Turner, 1972b

Xyloredo Turner, 1972b, p. 3. Type species: *Xyloredo nooi* Turner, 1972b, by original designation.

Mesoxylophaga Habe, 1977, p. 295. Type species: *Neoxylophaga teramachii* Taki & Habe, 1950.

Remarks: Turner (1972b) established the genus *Xyloredo* by distinguishing it from all the other xylophagines in having 1) a long, teredinid-like burrow with a calcareous lining, 2) a thin periostracal border of the tube, and 3) extended inhalant and exhalant canals. *Xyloredo* superficially resembles genera of the Teredinidae, but its anatomical features indicate placement in Xylophaginae; these features are: 1) the U-shaped wood-storing caecum, 2) the internal visceral mass completely covered by the shell, 3) the presence of mesoplax, and 4) the absence of apophysis and pallet (Turner, 1972b, 2002). Aside from the type species, Turner (1972b, 2002) included *Xyloredo ingolfia* Turner, 1972b and *Xyloredo naceli* Turner 1972b in this genus. We here include *Neoxylophaga teramachii* Taki & Habe, 1950 as the fourth species of this genus. Therefore, *Mesoxylophaga* is a junior synonym of *Xyloredo*.

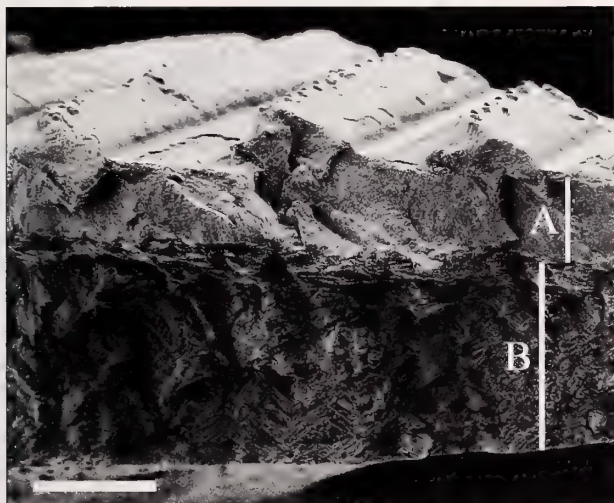


Figure 4. *Xyloredo teramachii*, enlarged view of sagittal section of the anterior slope. NSMT-Mo76706. Prismatic layer and crossed lamellar layer are indicated as A and B, respectively. Scale bar = 100 μ m.

Xyloredo teramachii (Taki & Habe, 1950)
[new combination]

(Figures 1–11)

Neoxylophaga teramachii Taki & Habe, 1950, p. 46, fig. 3; Kuroda et al., 1971, p. 715 (Japanese text), 471

(English text), pl. 121, fig. 11; *non* Okutani, 1968, p. 23, pl. 2, fig. 3.

Neoxylophaga (*Mesoxylophaga*) *teramachii*. Habe, 1977, p. 295.

Xylophaga teramachii. Hoagland & Turner, 1981, p. 44; Hoagland, 1983, p. 7; Turner, 2002, p. 227 (written as *Xylophaga teramachi* [sic]); Pailleret et al., 2007, p. 236, fig. 3.

Mesoxylophaga teramachii. Kuroda & Habe, 1981, p. 179, pl. 7, fig. 6; Higo & Goto, 1993, p. 670; Higo et al., 1999, p. 520; Higo et al., 2001, p. 181.

Xylophaga (*Mesoxylophaga*) *teramachii*. Okutani, 2000, p. 1031, pl. 513, fig. 3.

Shell: The valve is globose, up to 16.5 mm in height, 17.9 mm in length in the largest specimen, and has a shape typical of the subfamily, consisting of an anterior slope, disc and posterior slope (Figures 1–2). The valve surface is originally pearly white in color and glossy, and covered with a thin, dark golden brown periostracum over the whole surface (Figures 1, 8A). Finely denticulated bunches are regularly distributed over the anterior slope from the umbonal-ventral sulcus forwards, and fine growth lines extend over the disc and posterior slope. The posterior slope is widely reflected dorsally and its ventral midline, where the shelf terminates with the posterior slope and forms a blunt angulation (Figure 3). Since the margin of posterior

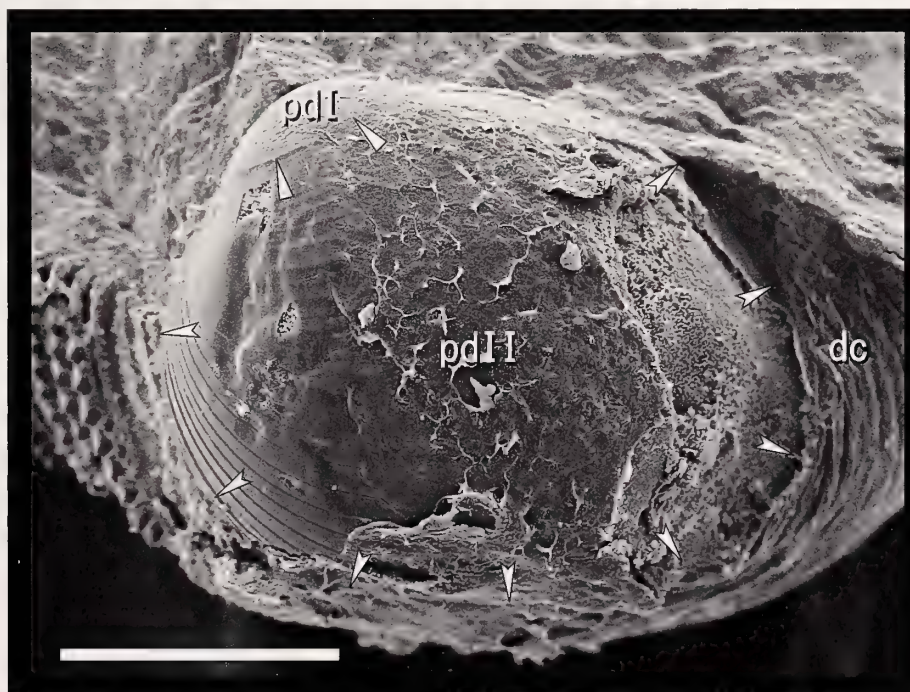


Figure 5. Prodissoconch of *Xyloredo teramachii*. NSMT-Mo76706. Arrowheads indicate the boundaries among prodissoconch I, II, and dissoconch. Abbreviations: dc = dissoconch, pdI = prodissoconch I, pdII = prodissoconch II. Scale bar = 100 μ m.

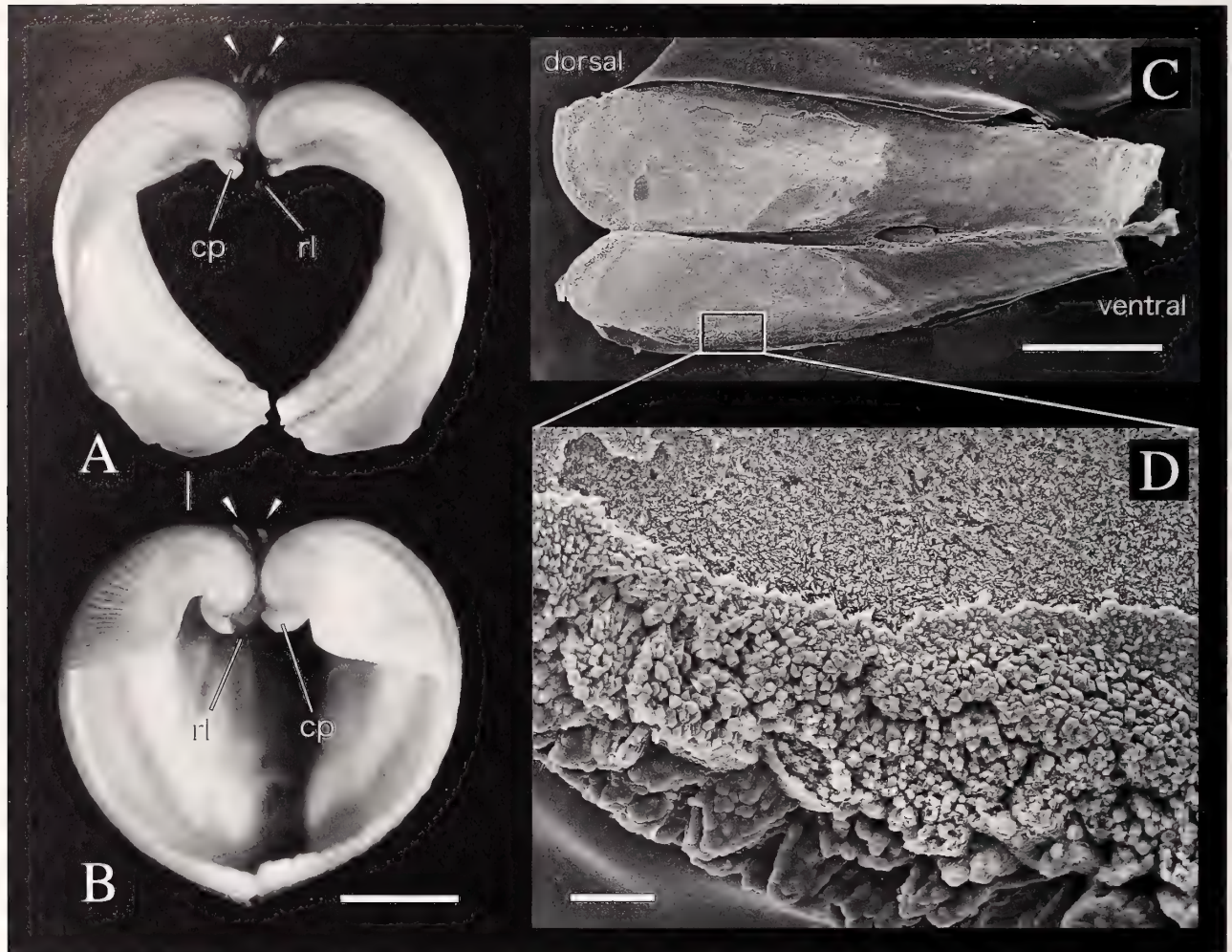


Figure 6. Mesoplax of *Xyloredo teramachii*. NSMT-Mo76706. A–B. Mesoplax *in situ* attached to the extended periostracum at the umbonal reflection indicated by arrowheads. C–D. Enlarged ventral view of the mesoplax. Abbreviations: cp = chondrophores, rl = rod-shaped ligament. Scale bars = A–B: 2 mm; C: 500 μ m; D: 20 μ m.

slope reflects laterally, the posterior end opens widely and large siphonal canals extend from it (Figure 6A). The umbonal-ventral sulcus (Figure 1A, C, G) is wide and concave without the crenate varix. The umbonal reflection largely develops and reflects dorsally, so that it is ear-shaped in anterior view (Figures 1E, 6B)

The internal valve surface is smooth, also pearly white and glossy. The shelf largely develops at the middle of the posterior slope and is impressed deeply to form a bump similar to that in terebinids (sf: Figure 3). The umbonal-ventral ridge (ubr: Figure 3) is wide, laterally depressed, irregularly marked with rough lines, descends from the umbo along the middle of the disc, and forms the large spherical ventral condyle (vc: Figure 3). In the left valve, the large, cuneiform and flat chondrophore is prominent beneath the umbo (cp: Figure 3), but in the right valve, the brown-

colored, rod-shaped ligament protrudes laterally (Figure 6B). The umbo strongly curves antero-ventrally (ub: Figure 3), and the prodissoconch is completely enclosed in the anterior reflection. The posterior muscular scar (pa: Figure 3) is large, deeply impressed with many lines, and divided into two areas: one with numerous irregular narrow lines that spread inward along the dorsal part of posterior slope (dorsal portion of posterior muscular scar: dpa, in Figure 3), and the other with a few wide lines that obliquely spread ventro-internally and are chevron-shaped ventrally (ventral portion of posterior muscular scar: vpa, in Figure 3). The pallial line (pl: Figure 3) is narrow and located along the valve margin, and is rather obscure near the ventral condyle. The accessory anterior adductor muscle scars (aca: Figure 3) and anterior adductor scars (aa: Figure 3) are rather obscure and

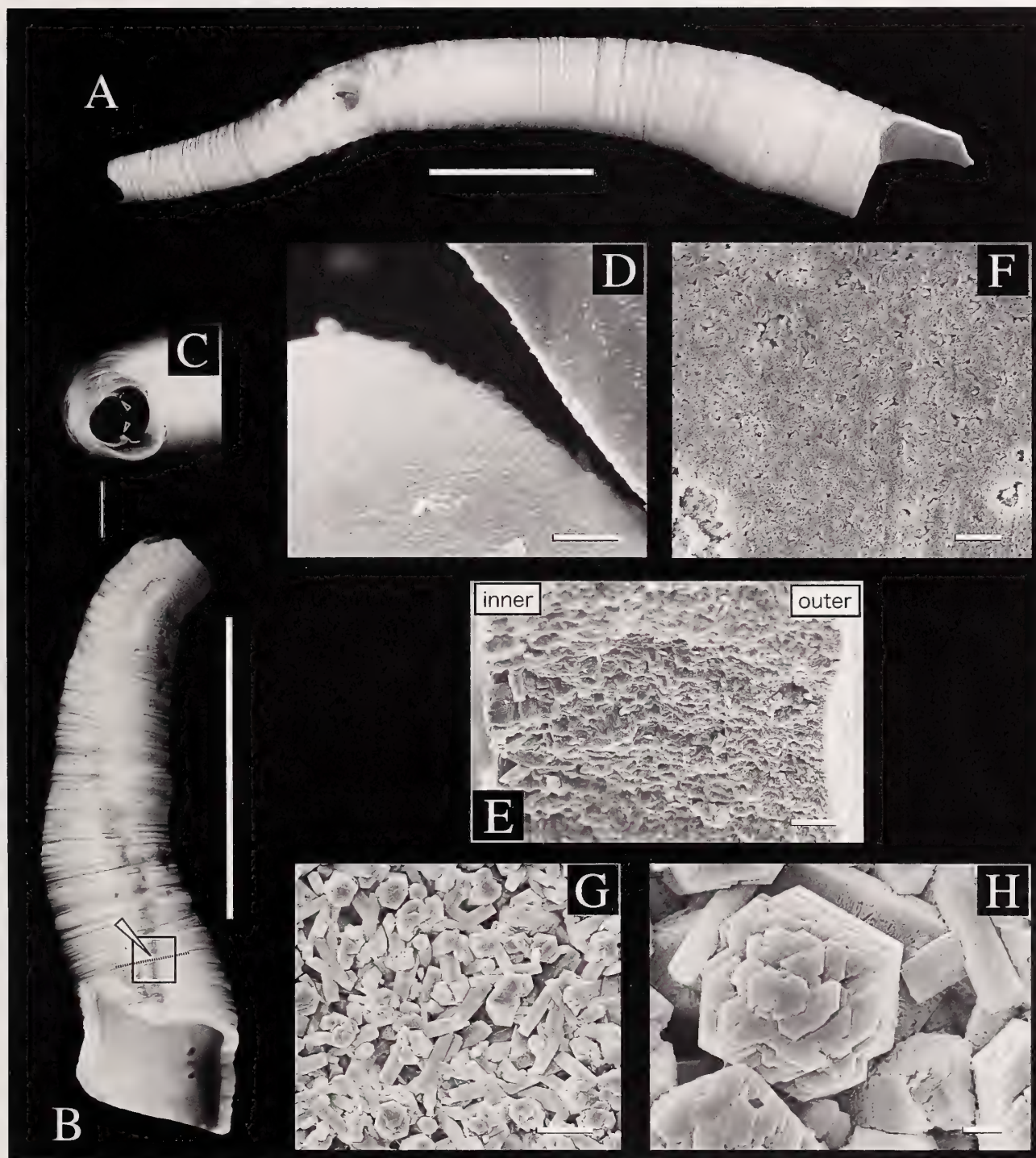


Figure 7. Calcareous tubes of *Xyloredo teramachii*. NSMT-Mo76706. A–B. Posterior end of the tube. Arrowhead, dotted line, and box indicate the enlarged views of D–H. C. posterior tip of the tube. Arrowheads indicate the lateral 'blades'. D. Enlarged view of periostracum which externally covers the tube. E. Enlarged view of sagittal section. F. Enlarged view of the outer surface. G–H. Enlarged view of the inner surface. Scale bars = A–B: 10 mm; D, F: 3 μ m; E, G: 10 μ m; H: 2 μ m.



Figure 8. Periostracal sheath of *Xyloredo teramachii* which covers the siphonal canals. NSMT-Mo76706. A. Intact specimen *in situ* with the complete periostracal sheath fully extended. B-C. Enlarged view of microscopic pores, indicated by arrowheads. Scale bars = A: 20 mm; B: 100 μ m; C: 10 μ m.

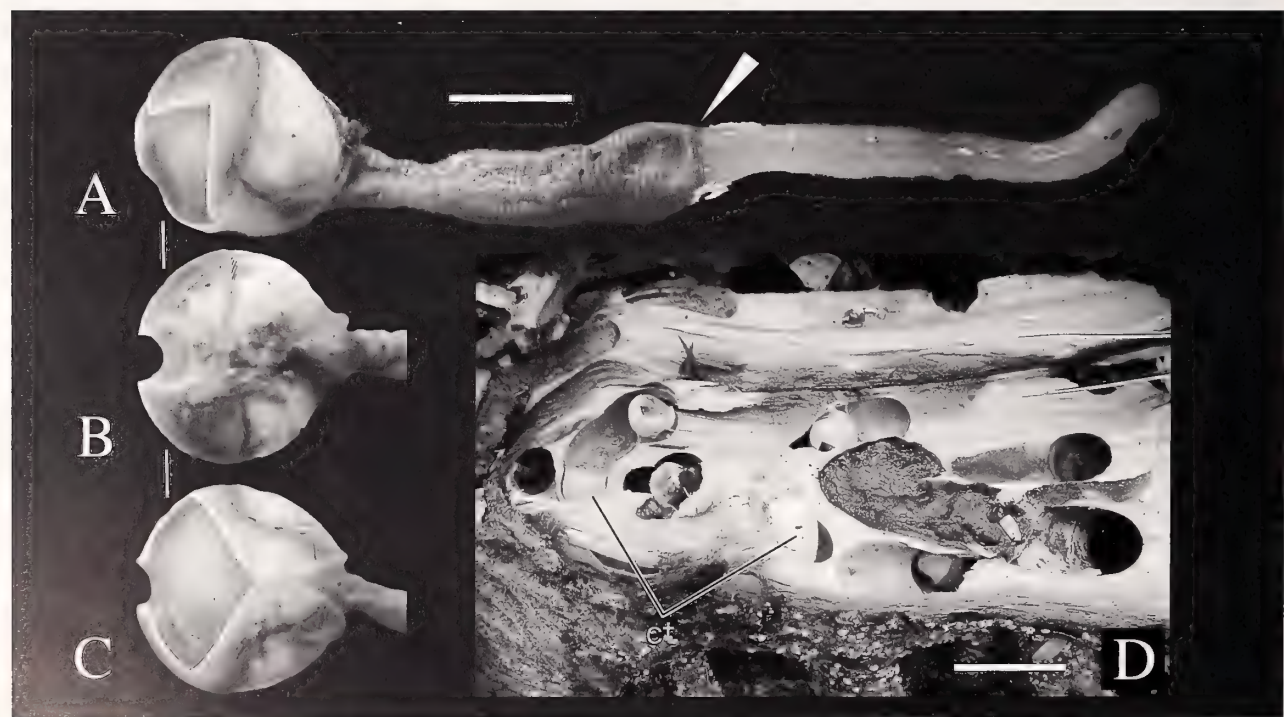


Figure 9. A-C. Animal *in situ* of *Xyloredo teramachii*. NSMT-Mo76706. Arrowhead indicates the boundary of the calcareous tube and the periostracal sheath. B. A sunken wood trunk *in situ* bored by *Xyloredo teramachii*. Abbreviation: ct = calcareous tube. Scale bars: A-C = 5 mm; D = 20 mm.

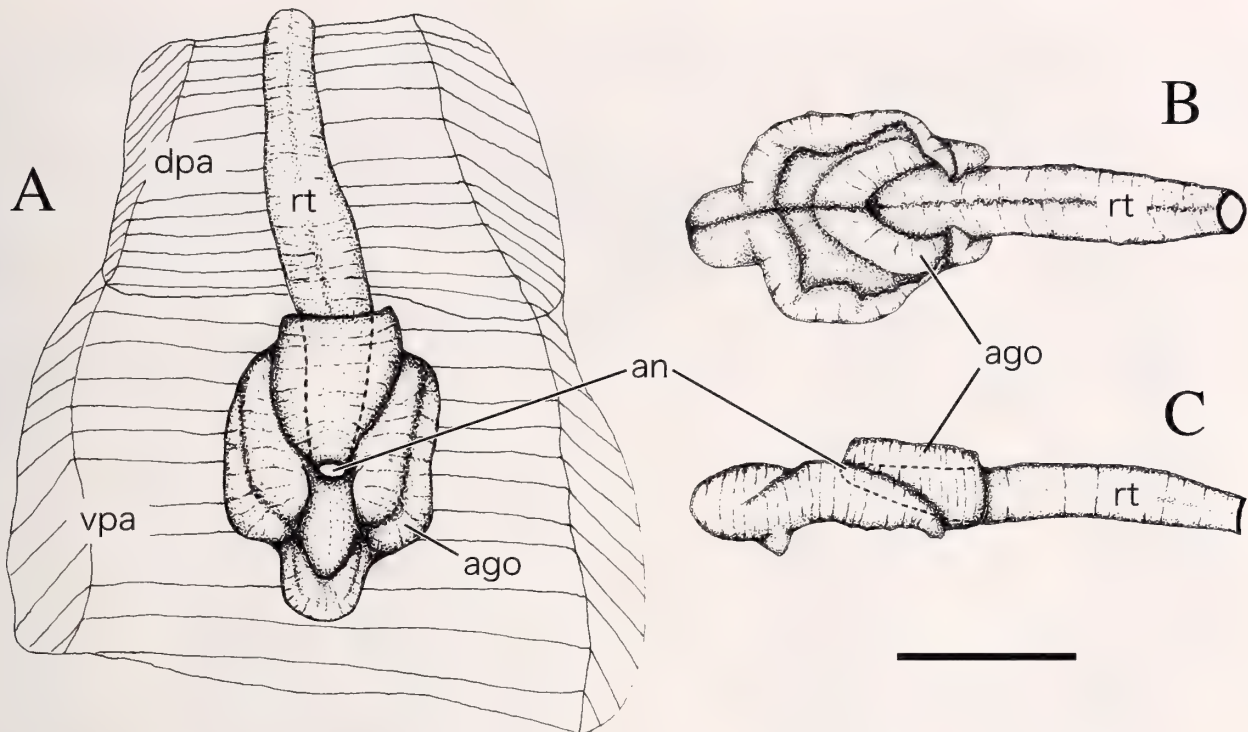


Figure 10. Accessory genital organ of *Xyloredo teramachii*. A. Posterior view. B. Anterior view. C. Lateral view. Abbreviations: ago = accessory genital organ, an = anus, dpa = dorsal portion of posterior adductor, rt = rectum, vpa = ventral portion of posterior adductor. Scale bar = 1 mm.

fuse with the pallial line; the former lies at the anterior margin of the anterior slope, and the latter are small and are located in the middle of the umbonal reflection. The posterior pedal retractor scar (ppr: Figure 3) is large, located close to the ventral portion of the posterior adductor scar, and positioned in the middle of the shelf. The anterior pedal retractor scar is situated beneath the anterior reflection. The ventral adductor scars and siphonal retractor scars are absent.

The valve is entirely of aragonite and consists of an outer, seemingly irregular simple prismatic layer, and an inner crossed-lamellar layer (Figure 4). Very thin prismatic sublayers, possibly of myostracal prisms, are occasionally inserted into the inner layer. This sublayer is also observed underneath the inner layer where the muscles adhere. The outer prismatic layer becomes thicker and forms denticles particularly in the anterior slope, and the crossed lamellar layer is prominent particularly in the strongly curved regions such as the umbo and the shelf. The umbonal-ventral ridge consists only of simple prisms.

Prodissoconch: The prodissoconch (Figure 5) is typical of planktotrophic development and composed of ca. 80 μm -long prodissoconch I (pdI: Figure 5) and ca. 205 μm -long prodissoconch II (pdII: Figure 5). It is totally concealed within the umbo due to the anterior

reflection and subsequently developed dissoconch in full-grown individuals. The surface is rather rough in prodissoconch I, while it is smooth and marked with regularly spaced concentric growth lines in prodissoconch II. The boundary between prodissoconch I and II is clearly marked with thin crenations (Figure 5, arrowheads).

Mesoplax: The mesoplax (Figure 6) is paired, tiny, long, subquadrangular (widening posteriorly), and slightly calcified. It is situated beneath the posteriorly ascended periostracum that covers the large and oval anterior incision latero-anteriorly (Figure 6A–B). The mesoplax consists of granular prisms with ca. 20 μm -wide subunits (Figure 6C–D). This structure is difficult to observe in live specimens because of their tiny size and the complete coverage with mucous debris (Figure 9B).

Burrow and calcareous tube: The long burrow (Figure 9D) is typical of teredinids, but does not produce ‘nodules,’ indicative of the switch-backed drilling behavior observed in teredinids. The approximate posterior two thirds of the burrow is lined with a calcareous tube (Figure 7) that is marked with distinct, regularly spaced growth rings (Figure 7A–B). The external surface of the tube is totally covered with a

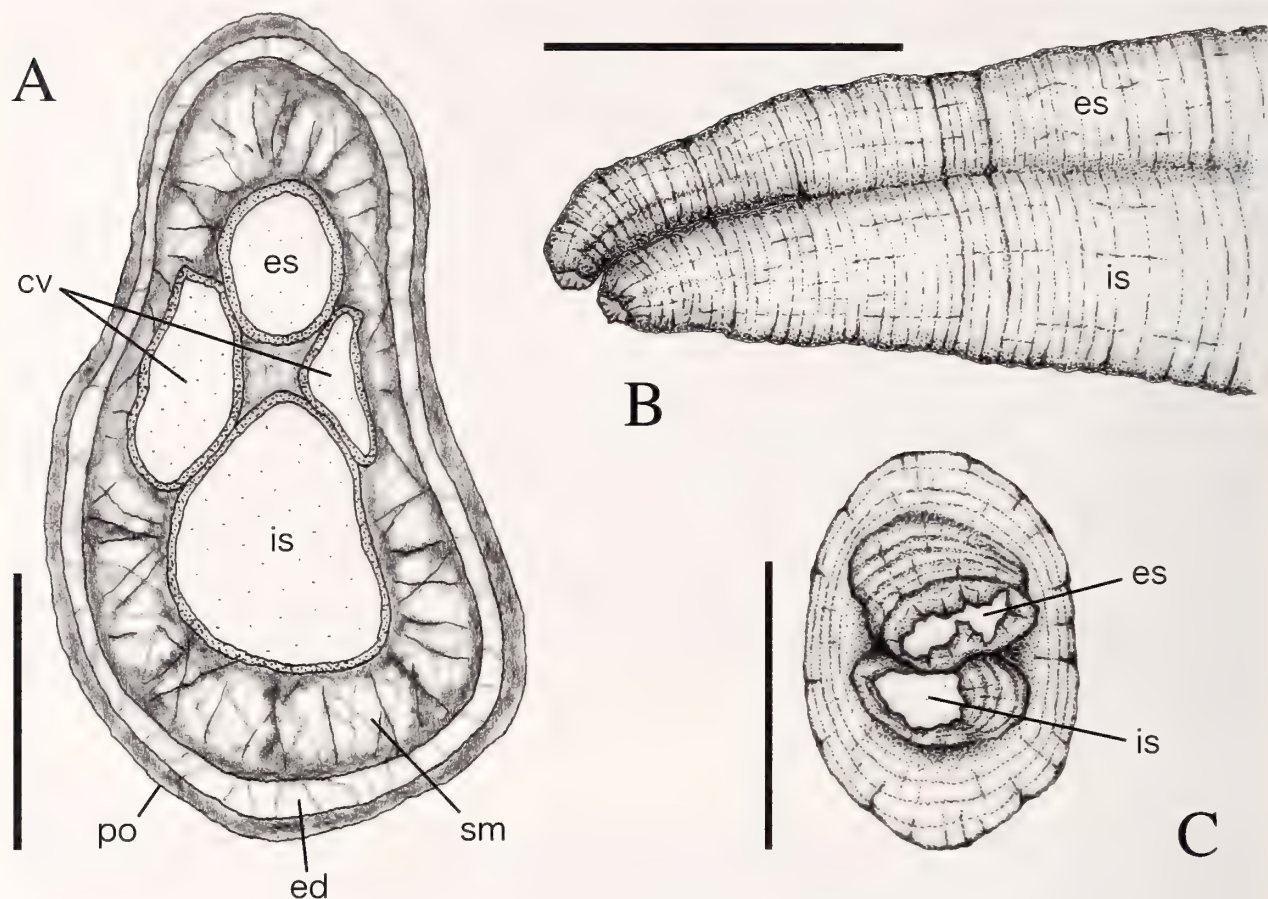


Figure 11. A. Sagittal section of the siphonal canals. B–C. Enlarged view of the siphons. Abbreviations: cv = cavity, ed = epidermis, es = exhalant siphonal canal and siphon, is = inhalant siphonal canal and siphon, po = periostracum, sm = sigmoid mesenchyme. Scale bars = 1 mm.

thin, smooth, and golden-glossy periostracum extending from the valve via a periostracal sheath (Figure 7D). The posterior portion of the tube is rather thick, and bears a lateral 'blade' internally at the tip in full-grown individuals (Figure 7C). From the posterior tip to the midpoint, the calcareous tube becomes significantly thinner, and is terminated with a dark-brown, strong demarcation (Figure 9A, arrowhead). The periostracal sheath extended from the valve also terminates at this demarcation (Figure 8A). The siphonal canal between the valve and calcareous tube is therefore solely covered with a periostracal sheath. The surface of periostracal sheath is smooth, but with microscopic holes (inside of pore is ca. 50 μm in length) all over the surface (Figure 8B–C). These tiny pores are limited in distribution in the extended periostracal sheath. The tube is composed mostly of periostracum in very young individuals; however, calcification of the tube occurs first at the base of the siphon with simple prismatic structure as well as on the internal surface of the full-grown tubes. The calcareous tube is of

aragonite, and consists of alternating fine and coarse hexagonal prismatic fibers, oriented either vertically or horizontally (Figure 7G–H) which gradually become smaller in diameter and length towards the outer portion (Figure 7E–F). The vertical prismatic fibers are usually less than 10 μm in diameter, and larger and more abundant than the horizontal prismatic fibers.

Soft parts: The animal is long as in teredinids, but differs in having a completely internal visceral mass, a mesoplax at the anterior incision, and in the absence of apophysis and pallet (Figure 9A–C). The anatomical features are generally identical to xylophagines (e.g., Purchon, 1941; Turner, 2002): the posterior adductor muscle is large, divided into two parts, and the ventral part consists of chevron-shape fibers and occupies two thirds of the posterior adductor, while the dorsal part consists of irregularly arranged fibers and descends along the posterior slope. The anterior adductor is small, depressed dorso-ventrally and sinuous in the anterior reflection. The accessory anterior adductor is

small, situated beneath the anterior adductor, and consists of stout muscular fibers. The posterior pedal retractor is large and closely inserted into the midpoint of the posterior adductor. The anterior pedal retractor is attached within the deeper portion of the umbo. The ventral adductor and the siphonal retractor are absent. The foot is large, discoid, and is surrounded by circular muscles around its margin (Figure 9C). The gills are narrow, thick, laterally stout, and consist only of inner demibranchs.

The digestive tract, also typical of xylophagines, has a large U-shaped wood-storing caecum that is connected to the stomach on its left side. The intestine ascends along the anterior margin of the posterior adductor, penetrates the heart, then terminates as a simple anus, which is surrounded by the accessory genital organ (Figure 10). The accessory genital organ is well-developed, glandular, free from any adhesion to the posterior adductor, and superficially composed of two components: a blade surrounding the end of the rectum (Figure 10A), and a peduncle whose ventral end protrudes like a proboscis and is situated below the rectum (Figure 10B–C). A pair of *vesicula seminalis*, a flattened small lobule visible in pale yellow, is present laterally on the thin suspensory membrane of the ctenidium close to the posterior end of the pedal retractor.

The siphons (Figure 11B) are short, simple, and both tips are usually aligned with the same length; however, the tip of the exhalant siphon appears to be slightly longer in some individuals. The apertures in both siphons are roughly serrated (Figure 11C). The siphonal canals are long and are connected to the posterior part of the visceral mass and siphons. The inhalant and exhalant siphonal canals are supported by well-developed sigmoid mesenchymes (sm: Figure 11A). A pair of cavities (cv: Figure 11A), that probably act as a haemocoel, are situated laterally between the siphonal canals, and continuously extends antero-posteriorly from the bases of siphons and visceral mass.

Type locality: Tosa Bay, Kochi Prefecture, western Japan, ca. 100 fathoms deep.

Distribution: West Pacific along the Japanese mainland from Ibaraki Prefecture to Kochi Prefecture and Vanuatu in the south Pacific. Depth ranges from 125 to 580 m.

DISCUSSION

Our detailed study on the shells and soft parts shows that *N. teramachii* can be reallocated to the genus *Xyloredo*. *Xyloredo nooi*, *X. ingolfia* and *X. naceli* are all less than 10 mm in maximum shell length (Turner, 1972b), while the present species reaches up to ca. 18 mm. In addition to the large shell size, the present species is easily distinguished from the above three

species in having a laterally reflected and developed posterior slope and dark golden brown periostracum. Okutani (1968: p. 23) identified a specimen from a sunken timber obtained at a depth of 1,510 m in Sagami Bay as *Neoxylophaga teramachii* (but in the figure caption he indicated it as “*Neoxylophaga teramachii*” [sic]). We suggest however that this specimen seems to belong to another, yet undescribed species because it differs from the present species in having a large and thick mesoplax, a flattened umbonal-ventral sulcus, and a varix-like crenation in its posterior portion. Habe (1977) allocated *Neoxylophaga lobata* (Knudsen, 1961) and *N. knudseni* Okutani, 1975 to his subgenus *Mesoxylophaga*. These two species do not have the calcareous tube in the burrow and therefore cannot be referred to *Xyloredo*. Generic positions of these species still remain uncertain until anatomical details are clarified.

The present species is the first record of the genus *Xyloredo* in the West Pacific. *Xyloredo nooi*, *X. ingolfia* and *X. naceli* were reported from the Atlantic, East Pacific, and South Pacific, respectively, from depths of more than 1,500 m, and they were heretofore known only from their type localities (Turner, 1972b, 2002). Hoagland (1983) suggested oviparous development for the above three species, but the present species appears to undergo planktotrophic development judging from the size (ca. 80 μ m in length) of prodissococonch I (see Jablonski & Lutz, 1980). The wide distribution from Japan to Vanuatu of the present species is likely due to its planktotrophic larval transport.

Teredinidae and Xylophaginae have unique reproductive strategies. Turner (1968) and Turner & Johnson (1971) stated that Teredinidae and Xylophaginae studied so far exhibit protandrous hermaphroditism, and suggested self-fertilization for Xylophaginae. Purchon (1941) extensively studied the mechanism of self-fertilization in *Xylophaga dorsalis* (Turton, 1819), and observed spawned sperms deposited in the seminal receptacle via the accessory genital organ that functions to tangle flooded sperms. Hoagland (1983) mentioned that all species of *Xyloredo* lack the accessory genital organ. We nevertheless recognized this organ in the present species (Figure 10) and an undetermined species of *Xyloredo* from Japan. Therefore, our study confirms the presence of the accessory genital organ in *Xyloredo*. It seems likely that the present species also undergoes self-fertilization because of the presence of *vesicula seminalis* and an accessory genital organ. However, this conclusion must be confirmed by detailed histological study on individuals with different developmental stages.

We show that the calcareous tube of *Xyloredo* is composed of hexagonal prismatic fibers, composed of aragonite. The prisms are vertically and horizontally oriented across each other (Figure 7G–H), and its

Table 1

Mineralogical and morphological features of the calcareous tubes in *Xyloredo*, *Teredina*, and Teredinidae. Note that *Teredina* is extant genus.

Family	Genus	Mineralogy	Gross morphology	Surface morphology
Pholadidae	<i>Xyloredo</i> <i>Teredina</i>	aragonite ¹ aragonite ⁴	long, winded ^{1,2,3} long, straight ^{5,6}	maked by regular growth lines ^{1,2,3} smooth, gaped at dorsal and ventral ^{5,6}
Teredinidae		calcite and/or aragonite ^{4,7}	long, winded ^{5,8}	smooth ^{5,8}

References: ¹this study; ²Turner (1972b); ³Turner (2002); ⁴Bøggild (1930); ⁵Turner (1969); ⁶Kelly (1988); ⁷Carter (1980b); ⁸Turner (1966).

structure is referable to 'isolated crystal morphotypes' as defined by Carter (1980a) and Carter & Clark (1985). Carter (1980a) reported that this microstructure is seldom observed in bivalves, since it has rarely been discussed in detail (e.g. Bøggild, 1930). As far as we are aware, the aragonitic isolated crystal morphotypes in *Xyloredo* reported herein is a characteristic microstructure among the accessory calcareous tubes in bivalves.

In Pholadoidea, only wood-borers produce long calcareous tubes: those are the genus *Xyloredo* (Turner, 1972b, 2002), fossil genera *Teredina* Lamarck, 1818 and *Turnus* Gabb, 1864 (Turner, 1969; Kelly, 1988) in Pholadidae, and all members of the family Teredinidae (Turner, 1966, 1969). Their fossilized burrows were described under the ichnogenus *Teredolites* Leymerie, 1842, which is characterized by a large club-shaped morphology with a single aperture, and occurs in xylic substrata since the Mesozoic (Leymerie, 1842; Hatai, 1955; Turner, 1966; 1969; Bromley et al., 1984; Plint & Pickerill, 1985; Kelly, 1988). Identification of the trace makers for *Teredolites* is, however, generally difficult because the burrows usually do not preserve internally embedded body fossils such as valves and/or palletal structure (Plint & Pickerill, 1985). Polychaetes and boring isopods produce similar burrows in xylic substrata, but they never secrete calcareous tubes in their burrows (Gingras et al., 2004). Therefore, *Teredolites* with the calcareous tubes can be attributed to pholadoidean boring bivalves.

We suggest that *Teredolites* associated with fossilized calcareous tubes can be referred to a specific family or genus within Pholadoidea by analyzing the mineralogy and external tube morphology (Table 1). Namely, *Xyloredo* is characterized by having a winding, aragonitic tube with remarkably strong, regular growth lines on the surface. In *Teredina* (an odd tube-bearing fossil genus of Pholadidae with morphology convergent to Teredinidae), the tube is mostly straight and aragonitic in composition but its surface is smooth with two gapes at the dorsal and ventral portions in some individuals (Bøggild, 1930; Turner, 1969; Kelly, 1988). On the other hand, Teredinidae has a strongly winding, calcitic and/or aragonitic tube with a smooth

tube surface (Turner, 1966, 1969; Carter, 1980). *Turnus* is a poorly known fossil genus originally placed in Teredinidae (Gabb, 1864; see also Turner, 1969) mostly from the Cretaceous. Kelly (1988) reported a lined calcareous *Teredolites* associated with valves of *Turnus kotickensis* Kelly, 1988, and tentatively referred the genus to Pholadidae. However, the systematic position of *Turnus* remains unclear until mineralogical and microstructural information is available. In conclusion, the mineralogy and external morphology of calcareous tube provide useful criteria for identification of *Teredolites* from the Mesozoic and Cenozoic.

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A Note on *Strombus coronatus* Defrance, 1827 and *Strombus coronatus* Röding, 1798 (Mollusca: Gastropoda)

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Abstract. *Strombus coronatus* Defrance, 1827 is considered a *nomen protectum*, and the cerithiid *Strombus coronatus* Röding, 1798 is demonstrated to be a *nomen oblitum* in accordance with the ICZN Article 23.9.1. The Late Miocene to Early Pliocene *Strombus coronatus* Defrance is shown to belong to *Persististrombus* Kronenberg & Lee, 2007, and its relation with other Neogene strombids is briefly addressed. A lectotype for *Strombus coronatus* Defrance is designated.

Key Words: Gastropoda, Cerithiidae, Strombidae, *Persististrombus*, homonymy, Miocene, Pliocene.

INTRODUCTION

While reviewing literature in the course of our research on strombid taxa from the Miocene Central Paratethys Sea, the nominal taxon *Strombus coronatus* Defrance, 1827 was frequently encountered. Although the identity and stratigraphic range of this species varies considerably in the literature (ranging from Late Oligocene to Late Pliocene) this name is treated as the valid name for a species of the family Strombidae Rafinesque, 1815. Nevertheless, the binomen *Strombus coronatus* was first introduced by Röding (1798) for an extant Indo-Pacific cerithiid. At that time the generic concept of *Strombus* differed fundamentally from the modern usage, and an analogous situation exists involving *Strombus granulatus* Röding, 1798 (a cerithiid) and the strombid *Strombus granulatus* Swainson, 1822 (Kronenberg and Lee, 2005).

NOMENCLATURAL STATUS AND HISTORY

1. *Strombus coronatus* Röding, 1798

When introducing *Strombus coronatus*, Röding (1798:98, species 1270) referred to *Murex aluco* Gmelin (1791, sp. 134) and Martini (1777:figs. 1478–1479). Houbriek (1978:104–105) pointed out that Röding's (1798) reference to Martini (1777) involves two species, which are now established as *Pseudovertagus aluco* (Linnaeus, 1758) [fig. 1478 of Martini (1777)] and *Rhinoclavis vertagus* (Linnaeus, 1758) [fig. 1479 of

Martini (1777)] respectively. Although Houbriek (1978) did not explicitly designate a lectotype for *Strombus coronatus* Röding, 1798, he synonymized *Strombus coronatus* Röding, 1798 with *Murex aluco* Linnaeus, 1758 [= *Pseudovertagus aluco* (Linnaeus, 1758)] by stating: "I here restrict *Strombus coronatus* [of Röding, MH and GCK] to fig. 1478 and place it into the synonymy of *Pseudovertagus aluco* ..." (Houbriek, 1978:104–105). Röding's *S. coronatus* soon disappeared from the literature, and the authors know of no 20th century reference to this binomen as a valid species name.

2. *Strombus coronatus* Defrance, 1827

Defrance (1827) introduced the primary homonym *Strombus coronatus*, 29 yr after Röding, referring to the illustration of a fossil strombid illustrated in Walch (1768:116, pl. C (38), figs. 1–2). Walch (1768) described the shell as a rare species present in collection cabinets of the time and suggested that it was collected in the Turin region of Italy. Defrance (1827) provided an adequate description of the shell, compared its morphology briefly with the extant *Strombus gigas* Linnaeus 1758, and remarked that it is frequently found in the Siena region in Italy. He seems to have doubted the Turin origin suggested by Walch (1768) and emphasized that the origin of that specimen was unknown. Indeed, the large-sized species is very common in the Italian Pliocene and was already known to science in the 17th century when Aldrovandi (1648)

identified it as *Murex albus*. After the definition by DeFrance (1827), the nominate taxon was cited frequently from Pliocene deposits throughout the Mediterranean and Eastern Atlantic regions.

Unfortunately, the species name was also applied to several Miocene and even Oligocene specimens from central and southern Europe. Most notably among others, Hörnes (1856) and Hoernes & Auinger (1884) identified Middle Miocene specimens of what is here provisionally called the *Persististrombus lapugyensis-exbonellii* group as *Strombus coronatus* DeFrance, 1827. Subsequently, many stout and strongly sculptured fossil strombids with long shoulder-spines have been treated as *Strombus coronatus* (e.g., Baldi, 1973; Schultz, 1998).

3. *Strombus coronatus*, DeFrance, 1827 – a *nomen protectum*

Herein, we refer to the International Commission for Zoological Nomenclature (ICZN) Article 23.2, which pleads for nomenclatural stability and perpetuation of long-accepted names, and to ICZN Article 23.9.1. To our knowledge, the name *Strombus coronatus* Röding, 1798 has not been used as a valid name after 1899, which meets the requirements of ICZN Article 23.9.1.1. (“the senior homonym has not been used as a valid name after 1899”). ICZN Article 23.9.1.2. states that “the junior homonym has been used as its presumed valid name in at least 25 works, published by at least 10 authors in the immediately preceding 50 yr and encompassing a span of not less than 10 yr.” Accordingly, we document that *Strombus coronatus* DeFrance, 1827 was used between 1956–2006 in 33 papers by 33 authors (see references below), which meets the requirements of Article 23.9.1.2. Thus, we invoke ICZN Article 23.9.1 to make the name *Strombus coronatus* DeFrance, 1827, a *nomen protectum* and *Strombus coronatus* Röding, 1798 a *nomen oblitum*.

CURRENT STATUS OF *STROMBUS* *CORONATUS* DEFRANCE, 1827 – SYSTEMATICS AND PALEOBIOGEOGRAPHY

Recently, Kronenberg & Lee (2007) introduced *Persististrombus* (type species by original designation: *Strombus granulatus* Swainson, 1822) as a new genus for a group of strombids which experienced its acme in the European Miocene and is now represented by *Persististrombus latus* (Gmelin, 1791) in the African Eastern Atlantic Province and by *P. granulatus* (Swainson, 1822) in the Panamic Province.

Although this grouping would make *Persististrombus* seemingly paraphyletic (see the consensus tree presented by Latiolais et al. (2006:440)), we here advocate the possibility of a distinct lineage, with hardly any morphological change since the Early Miocene, with two distinct side branches, one leading to *Strombus*

(here used in the strict sense, i.e., represented by the Recent species *S. pugilis* Linnaeus, 1758 (type species); *S. alatus* Gmelin, 1792; *S. gracilior* Sowerby, 1825) and one to *Lobatus* Iredale, 1921 (type species by monotypy: *Strombus bituberculatus* Lamarck, 1822 = *Strombus raninus* Gmelin, 1791). Moreover, the tree presented by Latiolais et al. (2006) is a consensus tree, based on 325 bp nuclear histone H3, where indeed *P. granulatus* plots out as the sister taxon of *Strombus* s.s. (Latiolais, 2003:fig. 1). These clades are sister to *Lobatus* for 640 bp mitochondrial COI. *Strombus granulatus* plots out as sister taxon of *Lobatus* (Latiolais, 2003:fig. 2) and these two are sister to *Strombus* s.s.

Persististrombus is characterized by “... moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate.” (Kronenberg and Lee, 2007). *Strombus coronatus* fits within this definition except for its low, concave spire and the number of protoconch whorls. A preliminary analysis of the *Persististrombus lapugyensis-exbonellii* group (Harzhauser and Kronenberg in prep.) reveals that there is a gradual change in spire height, i.e., from high-spined specimens in the early Langhian to lower spired specimens in the Serravallian of the Central Paratethys. Therefore we allocate both *S. coronatus* and the Pliocene to Recent *S. latus* Gmelin, 1791 to *Persististrombus*. As the protoconch in all examined specimens was poorly preserved, the number of whorls may have been slightly higher than the approximately three observed by us (see below). On the other hand, reduction of the number of protoconch whorls may have occurred in the Proto-Mediterranean, which would call for a minor adjustment in the description of *Persististrombus* as far as the number of protoconch whorls is concerned.

Genus *Persististrombus* Kronenberg and Lee 2007

Numbers in front of references refer to citations which are relevant for ICZN Article 23.9.1.2 (references before 1958 are found in the text above).

Persististrombus coronatus (DeFrance, 1827)
nov. comb.

Pl. 1, Figures 1–5, 7–9

Murex albus Aldrovandi, 1648:472, fig. 2.

Porphyroides Lancisi, 1771:298, fig. 1.

stumpfgestachelte dicklippige Flügelschnecke Walch, 1768:116, pl. C (38), figs. 1–2.

***Strombus coronatus* DeFrance, 1827:124.**



Figures 1-2. Copy of the illustration of the lectotype (designated herein) of *Strombus coronatus* Defrance, 1827 in Walch (1768, pl. 38, figs. 1-2).

Figures 3-6. *Persististrombus coronatus* (Defrance, 1827). 3-5: Specimen 93(1790) present in NMB. 6: Label with NMB specimen. Figures 7-9. A typical representative of *Persististrombus coronatus* from the Lower Pliocene of Tresanti (Florence, Tuscany) in Italy (NHM Inv. A2576); dorsal view, ventral view, apical view.

Strombus coronatus Defrance, Rutsch, 1936:34–35.

- [1] *Strombus coronatus* var. *compressonana* Sacco, Erüal-Erentöz, 1958:38, pl. 4, figs. 2–3.
- [2] *Strombus coronatus* Defrance, Glibert, 1963:219.
- [3] *Strombus coronatus* Defrance, Compagnoni, 1964:259, fig. 6.
- [4] *Strombus coronatus* Defrance, Moroni & Paonita, 1964:12.
- [5] *Strombus coronatus* Defrance, Hecht et al., 1964:451.
- [6] *Strombus (Strombus) coronatus* Defrance, Symeonides, 1965:256, pl. 32, fig. 1.
- [7] *Strombus coronatus* Defrance, Palla, 1967:959, pl. 72, fig. 2.
- [8] *Strombus coronatus* Defrance, Mastroilli, 1969:pl. 5, fig. 2.
- [9] *Strombus coronatus* Defrance, Beneventi & Piccoli, 1969:17, pl. 2, fig. 1.
- [10] *Strombus (Strombus) coronatus* Defrance, Malatesta, 1974:219, pl. 17, figs. 1–7.
- [11] *Strombus (Strombus) coronatus* Defrance, Pavia, 1975:112, pl. 5, figs. 1–4.
- [12] *Strombus coronatus* Defrance, Fekih, 1975:111, pl. 33, fig. 1.
- [13] *Strombus coronatus* Defrance, Meco, 1977:56, pl. 14, fig. 2, pl. 15, fig. 2, pl. 16, figs. 1–2, etc.
- [14] *Strombus coronatus* Defrance, Martinell, 1979:123, pl. 3, figs. 5–6.
- [15] *Strombus coronatus* (Defrance), Akbulut, 1980:5.
- [16] *Strombus (Strombus) coronatus* Defrance, Brébion, 1983:165 (? see further below).
- [17] *Strombus coronatus* var. *percoronata* Sacco, Fererro-Mortara et al., 1984:138, pl. 21, figs. 2a–2c.
- [17] *Strombus coronatus* var. *perspinosana* Sacco, Fererro-Mortara et al., 1984:139, pl. 21, figs. 6a–6b.
- [17] *Strombus coronatus* var. *compressonana* Sacco, Fererro-Mortara et al., 1984:139, pl. 21, figs. 7a–7b.
- [18] *Strombus coronatus* (Defrance), Moscatelli, 1987:18.
- [19] *Strombus coronatus* Defrance, Cavallo & Repetto, 1992:58, fig. 101.
- [20] *Strombus coronatus* (De France), Falconeri, 1996:67–68, figs 1–9, 69 figs 1–9.
- [21] *Strombus coronatus*, Gregor et al., 1998:13 middle fig., specimen on right, 13 bottom fig.
- [22] *Strombus coronatus*, Ivanov et al., 2001:112 bottom figure, specimen on left.
- [23] *Strombus coronatus* (Defrance), İslamoğlu, 2002:53, 54.
- [24] *Strombus (Strombus) coronatus* Defrance, Landau et al., 2004:63, pl. 14, fig. 6.

non Persististrombus coronatus (Defrance, 1827)

[but used as presumed valid name as required by
ISCN Article 23.9.1.2.]

- [25] *Strombus (Str.) coronatus* Defrance, Sieber, 1958:141 (= *ex gr. Persististrombus exbonellii* Sacco, 1893).
- [26] *Strombus coronatus* Defrance, Strausz, 1966:222, figs. 102–103 (= *ex gr. Persististrombus lapugyensis-exbonellii* Sacco, 1893).
- [27] *Strombus coronatus* Defrance, Baldi, 1973:2705, pl. 34, figs. 7–8. (unnamed *Persististrombus*).
- [28] *Strombus coronatus* Defrance, Steininger & Baldi, 1975:345, pl. 3, fig. 6. (unnamed *Persististrombus*).
- [29] *Strombus (Strombus) coronatus* Defrance, Tanar, 1985:22, pl. 1, fig. 4 (= *Melongenella cornuta* Agassiz, 1843).
- [30] *Strombus (Strombus) coronatus* Defrance, Nikolov, 1993:69, pl. 3, figs. 7–8 (= “*Euprotomus*” *schroedingeri* Hörnes in Hoernes & Auinger, 1884).
- [31] *Strombus (Strombus) coronatus* Defrance, Schultz, 1998:60, pl. 23, fig. 6 (= *ex gr. Persististrombus lapugyensis* Sacco, 1893).
- [32] *Strombus coronatus* (Defrance), Árpád, 2003:11 (= *ex gr. Persististrombus bonellii* Brongniart, 1823).
- [33] *Strombus coronatus* (Defrance), İslamoğlu & Taner, 2003:22 (= *ex gr. Persististrombus bonellii* Brongniart, 1823).

Note that the suggested affiliations are only preliminary; details will be provided in Harzhauser and Kronenberg in prep.

Defrance (1827:124) based his description of *Strombus coronatus* on figures in Walch (1768, pl. 38 figs 1–2; attributing the work to Knorr) and added “On trouve des coquilles de cette espèce aux environs de Sienne.” (One finds shells of this species near Siena). We conclude that Defrance’s description is based on both the illustration by Walch and by specimens from near Siena (Italy) Defrance had seen prior to his description. These specimens are best considered syntypes of *Strombus coronatus* (ICZN recommendation 73F). Dance (1986:209) gives information on the Defrance collection, stating it is present in the Musée d’Histoire Naturelle, Caen (France), and some shells in Geneva (Switzerland).

According to Cleevely (1983), the Defrance collection in Caen was destroyed in 1944. It is however possible that parts of the Defrance collection, such as parts of the Coelentrata (see Cleevely, 1983), survived this bombing and the whereabouts of possible remains are presently unaccounted for. Nevertheless, Dr. Jean-Philippe Rioult, Université de Caen confirmed to Mr. Franck Frydman (email 13 November 2007) that the Defrance collection indeed was destroyed (“... mais cette collection a bien été détruite en totalité lors du bombardement incendiaire des locaux du Muséum d’Histoire Naturelle de Caen le 7 juillet 1944.”) and added “A moins d’un miracle (...) il ne faut pas compter retrouver d’échantillons de cette collection.”

Dr. Yves Finet, Muséum d’Histoire Naturelle,

Genève (MHNG), informed us that there are no specimens of *S. coronatus* present in that museum (email 25 Oct. 2007).

Rutsch (1936) claimed that the specimen present in the collection of the Naturhistorisches Museum Basel (NMB), coll. nr. 93/1790, is the specimen illustrated by Walch. However, comparison of images of the Basel specimen, kindly made available by Mr. Arne Ziems, NMB, here reproduced (Figures 3–5), clearly demonstrates that these are different specimens. Also the accompanying label (Figure 6) makes a provenance from the Walch collection quite improbable.

Therefore, the only currently available syntype is the specimen illustrated by Walch (1769), and all other syntypes are considered lost.

Meco (1977) distinguished *S. coronatus* from *S. latus* Gmelin, 1791 (as *S. bubonius* Lamarck, 1822) based on morphometrics, without fixing a type specimen for *S. coronatus*. Prior to Meco's (1977) publication, *S. coronatus* had been often confused with other species of the Miocene to Recent which we allocate to *Persististrombus*. Even after Meco's (1977) paper (see listing above) considerable confusion about the identity of *S. coronatus* remains.

To unequivocally stabilize the identity of *S. coronatus* we hereby designate the specimen illustrated in Walch (1768, pl. 38, figs 1–2), here re-illustrated (Figures 1–2), as lectotype of *Strombus coronatus* Defrance, 1827.

Description: Protoconch of all available specimens poorly preserved, with about 3 smooth, moderately convex whorls. Shell of Pliocene specimens very thick and heavy; Tortonian ones are generally slightly less robust. Spire low, concave, with an average apical angle of 70.8° ($n = 47$, $s = 11.0$; Table 1) [apical angle = angle of spire whorls; body whorl angle = angle between the flanks of the terminal part of the last whorl; body whorl height = height of last whorl from anterior tip to the suture between last whorl and last spire whorl in apertural view]. Size of adults usually up to 110 mm, but giant representatives may attain sizes up to 155 mm; dwarf forms are also common. About eight prominent triangular shoulder spines on body whorl and evident on the spire whorls as sutural excrescences which produce a stellate ("coronate") pattern in apical view. Two more spiral rows of knobs on the body whorl; middle one often reduced or absent while anterior one predominates. Outer lip solid and strongly thickened. Columellar callus thick, covering the base completely in fully grown adults. Often wing extends apically above the suture between the penultimate and body whorls. Stromboid notch deeply incised and regularly U-shaped. A typical specimen of *S. coronatus* is illustrated here (Figures 7–9).

Remarks: Herein we treat only Late Miocene to Early

Pliocene specimens as *Persististrombus coronatus* (Defrance, 1827). Several morphologically similar specimens known from Early to Middle Miocene deposits of the Paratethys Sea usually have been treated as *Strombus coronatus* Defrance. However, these shells differ in their stromboid notch-morphology (e.g., shallower and less well defined margins) and/or in their higher early spire. Sacco (1893) recognized these differences and introduced several new species names for such specimens. These "coronatus-like" morphs represent independent, iterative developments within a *Persististrombus* lineage which comprise a herein-proposed preliminary concept: the *Persististrombus lapugyensis-exbonellii* group. A slender counterpart of iterative but unrelated developments is represented by the extant *Persististrombus granulatus* (Swainson, 1822) and the Middle Miocene *Persististrombus exbonellii* (Sacco, 1893). Occurrences of *Persististrombus* in the Pontilevian fauna (Middle Miocene) of the Loire Basin described by Glibert (1949) as *Strombus coronatus* might also belong to this group. A detailed analysis of the Middle Miocene strombids will be presented elsewhere (Harzhauser & Kronenberg in prep.).

Distribution: The earliest record of this species is mentioned by Brébion (1983) from the Middle or Late Miocene of Angola. Unfortunately, Brébion (1983) did not provide a description or an illustration. Therefore, this interesting occurrence has to be treated with caution. If the identification is correct, then the West African Miocene occurrence of *Persististrombus coronatus* suggests that this species is a West African element, which later invaded the Mediterranean Region. There, it does not appear before the Tortonian, where it is known from Italy and Turkey (Sacco, 1893; Stchepinsky, 1939, 1946). It is apparently absent from the Mediterranean during the Messinian but flourished in this bioprovince in the Zanclean and the early Piacenzian. During this warm period the species is recorded from Portugal, Spain, France, Italy, Greece, Turkey, Syria, Libya, Tunisia, Morocco and the Canary Islands (Pereira da Costa, 1866; Almera & Bofill, 1886; Serres, 1829; d'Ancona, 1871; Sacco, 1893; Gignoux, 1913; Erünel-Erentöz, 1958; Symeonides, 1965; Roman, F. 1940; Fekih, 1975; Lecointre, 1952; Landau et al., 2004; Meco, 1977). *Persististrombus coronatus* disappears from the Mediterranean Sea completely with the onset of the Late Pliocene cooling (Landau et al., 2004) and seems to be extinct thereafter.

CONCLUSIONS

Despite its homonymy with a cerithiid described by Röding (1798), *Strombus coronatus* Defrance, 1827 can be conserved as a name for a Miocene to Pliocene strombid species. A review of the literature fulfills the requirements of the ICZN. Moreover, recent studies of

Table 1

Measurements of 47 specimens of *Persististromus coronatus* (Defrance, 1827) from the collections of the Natural History Museum Vienna (NHM) and Naturalis - Nationaal Natuurhistorisch Museum, Leiden (RGM).

nr.	locality	dating	height (mm)	width (mm)	aperture height (mm)	body whorl height (mm)	apical angle	body whorl angle
1	Muezzinler - Turkey	Late Miocene	42	21	27	29	65	32
2	Muezzinler - Turkey	Late Miocene	29	14.5	19	22	56	39
3	Muezzinler - Turkey	Late Miocene	44	23	27	28	50	43
4	Muezzinler - Turkey	Late Miocene	43	22	28	31	71	42
5	Muezzinler - Turkey	Late Miocene	40	20	25	29	65	35
6	Muezzinler - Turkey	Late Miocene	41	22.5	29	30	63	38
7	Muezzinler - Turkey	Late Miocene	85	75	83	71	63	31
8	Muezzinler - Turkey	Late Miocene	75	50	57	60	62	40
9	Muezzinler - Turkey	Late Miocene	64	66	46	48	65	39
10	Muezzinler - Turkey	Late Miocene	65	33	48	49	59	35
11	Bolognese - Italy	Early Pliocene	64	50	60	54	62	31
12	Bordighera - Italy	Early Pliocene	58	50	49	48	60	33
13	Bucciana - Italy	Early Pliocene	85	78	78	74	75	37
14	Toscana - Italy	Early Pliocene	86	75	87	79	72	41
15	Toscana - Italy	Early Pliocene	69	60	56	57	73	40
16	Asti - Italy	Early Pliocene	93.5	70.5	84.5	83	66	38
17	Asti - Italy	Early Pliocene	108.4	94.8	111.5	98.5	85	40
18	Asti - Italy	Early Pliocene	103	85	103.4	97.5	78	40
19	Castell Arquato - Italy	Early Pliocene	69.9	54.5	70	66.9	88	36
20	Castell Arquato - Italy	Early Pliocene	101.5	87.7	95.9	89	66	47
21	Castell Arquato - Italy	Early Pliocene	111.8	95.6	108.8	101.3	85	37
22	Castell Arquato - Italy	Early Pliocene	104	88	94	89.9	72	40
23	Ceriale Rio Torsero - Italy	Early Pliocene	49	34	36	30	60	30
24	Ceriale Rio Torsero - Italy	Early Pliocene	65	47	54	47	62	34
25	Ceriale Rio Torsero - Italy	Early Pliocene	65	44	53	48	65	35
26	Ceriale Rio Torsero - Italy	Early Pliocene	70	43	55	53	57	34
27	Ceriale Rio Torsero - Italy	Early Pliocene	51	35	47	33	75	36
28	Ceriale Rio Torsero - Italy	Early Pliocene	65	61	46	45	63	32
29	Ceriale Rio Torsero - Italy	Early Pliocene	65	54	49	47	61	35
30	Ceriale Rio Torsero - Italy	Early Pliocene	73	56	56	46	68	37
31	Ceriale Rio Torsero - Italy	Early Pliocene	115	94	85	72	84	37
32	Ceriale Rio Torsero - Italy	Early Pliocene	104	102	81	83	85	36
33	Siena - Italy	Early Pliocene	65.3	59.7	61	56.6	62	41
34	Siena - Italy	Early Pliocene	62.8	49	55.7	55.1	85	35
36	Siena - Italy	Early Pliocene	98	98	84	82	75	38
37	Siena - Italy	Early Pliocene	78	75	77	58	80	33
38	Tresanti - Italy	Early Pliocene	100.8	83.3	94.2	89.5	74	37
39	Tresanti - Italy	Early Pliocene	108.5	84	105.7	93	67	40
40	Tresanti - Italy	Early Pliocene	111.7	87	110	98	87	40
41	Tresanti - Italy	Early Pliocene	98.4	90	103.4	89	70	39
42	Tresanti - Italy	Early Pliocene	95.4	84	92.5	84	64	40
43	Sicily	Early Pliocene	100.9	95.8	94.4	88.5	67	38
44	Sicily	Early Pliocene	90	84.4	87.2	78	65	40
45	Fuerteventura - Canary Islands	Early Pliocene	137	126	135	115	78	36
46	Fuerteventura - Canary Islands	Early Pliocene	111	112	112	105	85	40
47	Fuerteventura - Canary Islands	Early Pliocene	134	122	130	125	78	38

Kronenberg & Lee (2007) have shown that this taxon is assignable to the strombid genus *Persististrombus*, which affiliation unites a conspicuous amphi-Atlantic Neogene species flock. The fossil record suggests that *Persististrombus coronatus* might have its roots in the Miocene of West Africa. During the Tortonian it managed to invade the Mediterranean Sea. The Messinian crisis forced the species to retreat from the Mediterranean, and it might have found a refuge in the Eastern Atlantic. During the early Pliocene warming it became very abundant throughout the Mediterranean, being recorded from nearly all coasts. Its final extinction was related to the Pliocene cooling. This strict species concept shows that the Early and Middle Miocene populations of Central Europe, erroneously synonymized with *P. coronatus* in the literature, represent “*coronatus*-like” but unrelated morphs of the *Persististrombus lapugyensis-exbonellii* group.

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Pliocene and Pleistocene *Fissurella* Bruguière, 1789 (Gastropoda: Fissurellidae) from Southern Peru

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Abstract. Twelve species of fossil Pliocene and Pleistocene keyhole limpets, *Fissurella* (*Fissurella*), from southern Peru are reported, including four new species: *Fissurella aranea*, sp. nov., *F. geoglypha*, sp. nov., *F. mcleani*, sp. nov., and *F. persica*, sp. nov. These species and others from Peru and Chile are assigned to several morphological species groups that are nearly congruent with clades defined by DNA sequences (Olivares, 2006). *Fissurella* (*Fissurella*) probably appeared in western South America during the late Miocene or soon thereafter, possibly from the western Pacific Ocean or South Africa, with major clades in existence in Peru by the late early Pliocene. A late Pliocene extinction of some fissurellid species and the subsequent addition of new and often larger species in Peru, Chile, and Argentina has produced the modern diverse *Fissurella* (*Fissurella*) fauna.

INTRODUCTION

In a systematic treatment of South American keyhole limpets assigned to *Fissurella* (*Fissurella*) Bruguière, 1789, McLean (1984a) lamented their limited fossil record in western South America, a record comprised only of Philippi's (1887) description of one Pliocene species from Chile, *F. concolor* Philippi, 1887, Herm's (1969) list of Pleistocene species and passing mention of Pliocene *Fissurella* from Chile, and McLean's own figures of Pliocene *F. concolor* and *Fissurella* sp., cf. *F. crassa* Lamarck, 1822, both also from Chile.

This article augments that sparse record with an account of *Fissurella* in Pliocene and Pleistocene strata from southern Peru, including the extant *F. maxima* Sowerby, 1835, *F. limbata* Sowerby, 1835, *F. crassa*, *F. latimarginata* Sowerby, 1835, and the extinct *F. concolor*, which were found in a Pliocene outcrop near the coastal town of Chala, as were two new species, *F. persica*, sp. nov., and *F. aranea*, sp. nov. A specimen of *F. pulchra* Sowerby, 1835, was found in a nearby Pliocene deposit and a worn specimen of *F. cumingi* Reeve, 1849, was discovered on a nearby middle Pleistocene marine terrace. A Pliocene exposure above the Río Acarí has yielded specimens of *F. concolor*, *F. persica*, and the extant *F. peruviana* Lamarck, 1822. Pliocene sandstones near Yauca produced single specimens of the extinct *F. mcleani*, sp. nov., and *F. geoglypha*, sp. nov. The northernmost record for any South American *Fissurella* (*Fissurella*) is formally reported, a Pliocene specimen of *F. peruviana* from northern Peru.

GEOLOGY

The Cenozoic stratigraphy of southern Peruvian forearc basins (Figure 1) was reviewed by DeVries (1998). Pliocene marine deposits of the Pisco and La Planchada formations include bioclastic sandstones and balanid coquinas (Beudet et al., 1976; Muizon & DeVries, 1985), the remnants of littoral deposits that lapped onto pre-Eocene crystalline platforms or accumulated at the foot of steep cliffs of the Andes Cordillera.

Two outcrops of *Fissurella*-bearing Pliocene strata warrant mention. Bioclastic debris of the La Planchada Formation crops out along sweeping curves of the Panamerican Highway southeast of Chala where the road descends to the strandline at Playa Huacllaco (Figure 2). The sediments accumulated in high-energy foreshore and rocky intertidal environments in front of a rugged coastline of igneous rock (DeVries, 2003). The age of the Huacllaco beds is constrained by basal beds containing specimens of the muricid gastropods *Concholepas nodosa* Möricke, 1896, *Acanthina triangularis* DeVries, 2003, and *Hermespina mirabilis* (Möricke, 1896), which collectively indicate a late early to early late Pliocene age (DeVries & Frassinetti, 2003), and by the uppermost and oldest marine terrace, whose elevation and largely extant taxa, including *Acanthina unicornis* (Bruguière, 1789) and *Concholepas concholepas* (Bruguière, 1789), suggest a latest Pliocene age (Muizon & DeVries, 1985; DeVries, 1995, 2000, 2003). Four lithologic units were designated in the Huacllaco section: Unit I (crossbedded balanid coquina, late early Pliocene), Unit II (bioclastic sandstone and polychaete reefs, late early or early late Pliocene), Unit III (ferruginous cobble-bearing bioclastic sandstone, early late Pliocene), and Unit IV (conglomerates and massive coquina beds, late late Pliocene).

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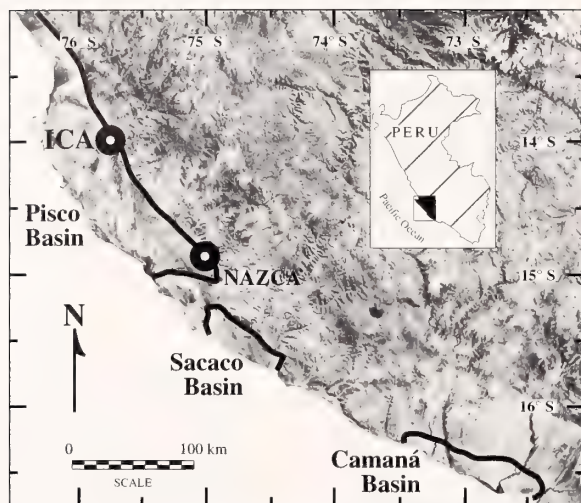


Figure 1. Location of forearc basins (Pisco, Sacaco, Camaná) along the coast of southern Peru.

The second notable outcrop lies east of Chauviña, set back from the southeastern rim of the Río Acarí, where small knobs of bedded strata constitute a condensed section of lower Pliocene to uppermost Pliocene bioclastic sandstone and coquina (Figure 3). The Acarí section has a basal lag of igneous boulders with mollusks (*Hermiopsis saskiae* DeVries & Vermeij, 1997, *Trophon carlosmartini* DeVries, 2005, and *Xanthochorus ochuroma* DeVries, 2005) that indicate an early Pliocene age (DeVries & Vermeij, 1997; DeVries, 2005a, 2005b). Beds five and six meters above the boulders contain *Concholepas kieneri* Hupé, 1854, and *Anadara* aff. *A. chilensis* (Philippi, 1887), as well as the aforementioned muricids, collectively indicating a somewhat later early Pliocene age (Muizon & DeVries, 1985; DeVries, 1995, 2000). Beds nine and 11 m above the boulders with *Concholepas camerata* DeVries, 2000, *Stramonita chocolata* (Duclos, 1832), *Xanthochorus xuster* DeVries, 2005, and *Xanthochorus cassidiformis* (Blainville, 1832), indicate a late Pliocene age (DeVries, 2000, 2005a, 2007). An overwhelming preponderance of extant molluscan taxa (e.g., *Concholepas concholepas* and *Xanthochorus cassidiformis*) in the uppermost coquinas, coinciding with the most elevated and oldest marine terrace, indicate a latest Pliocene age (Muizon & DeVries, 1985).

MATERIALS AND METHODS

Specimens of fossil *Fissurella* described in this study were found by the author. Most fossil examples had lost their aragonitic inner layer, so features of the external calcitic layer (shape, radial and concentric sculpture, ray patterns, margin width and coloration)

became the principal means for diagnosing species, with greatest emphasis placed on radial sculpture.

Comparative fissurellid material came from the Natural History Museum of Los Angeles County (LACM) and the author's personal collection. Selected citations are given for known species, emphasizing those that post-date McLean (1984a).

Locality and sample descriptions are listed in the appendix. Lengths (L), widths (W) and heights (H) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Some figured specimens are coated with ammonium chloride; others are shown with transmitted light to reveal color patterns. Types and other numbered specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM), the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru (MUSM INV) and in the case of one specimen of *Fissurella peruviana*, the Orton Geological Museum, The Ohio State University (OSU).

SYSTEMATIC PALEONTOLOGY

Family Fissurellidae Fleming, 1822

Subfamily Fissurellinae Fleming, 1822

Genus *Fissurella* Bruguière, 1789

Subgenus *Fissurella* Bruguière, 1789

Type species (by monotypy) *Patella nimbose* Linnaeus, 1758. Recent, Caribbean.

Discussion: McLean (1984a) included within *Fissurella* (*Fissurella*) all fissurellid gastropods with an aragonitic inner shell layer and calcitic outer shell layer, i.e., 13 South American taxa and two species from the northern hemisphere, *F. (Fissurella) volcano* Reeve, 1849 (California), and *F. (Fissurella) nimbose* (Linnaeus, 1758) (Caribbean Sea, Brazil). Stuber (1991) supported the monophyly of *Fissurella* (*Fissurella*) *sensu* McLean (1984a), but Olivares (2006) did not, concluding instead that molecular data showed *F. nimbose* to be more closely related to the eastern Atlantic *F. (Cremides) schrammi* Fischer, 1857, than South American species of *Fissurella* (*Fissurella*). Until molecular data become available for *F. volcano*, McLean's (1984a) definition of *Fissurella* (*Fissurella*) will be utilized here, with the caveat that removing both *F. volcano* and *F. nimbose* from the subgenus would result in a South American subset of *Fissurella* equivalent to Pérez-Farfante's (1943) imperfectly diagnosed *Fissurella* (*Balboaina*).

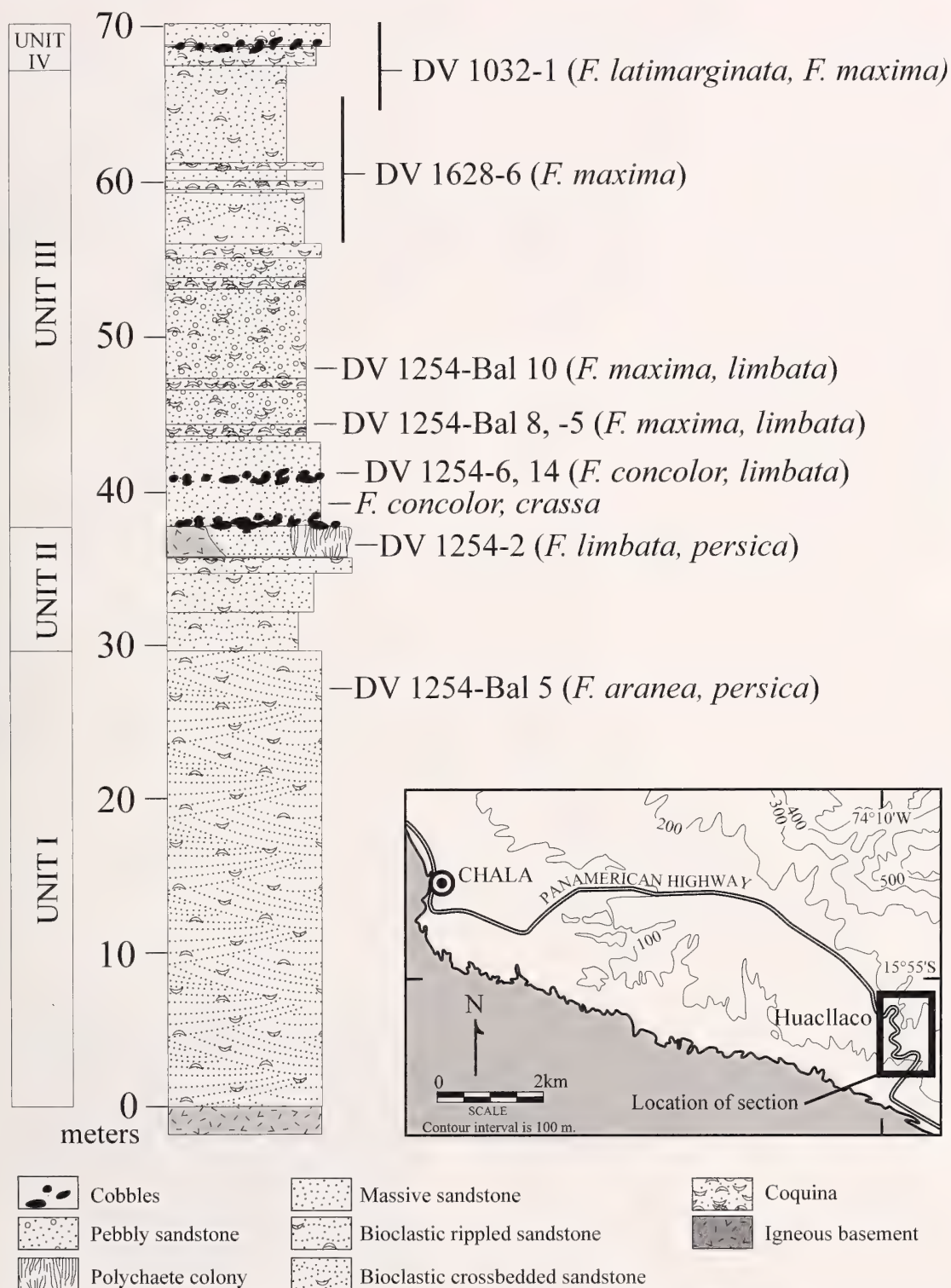


Figure 2. The Huacllaco lithologic section southeast of Chala, type locality of *Fissurella aranea*, sp. nov. The location map is shown in inset.

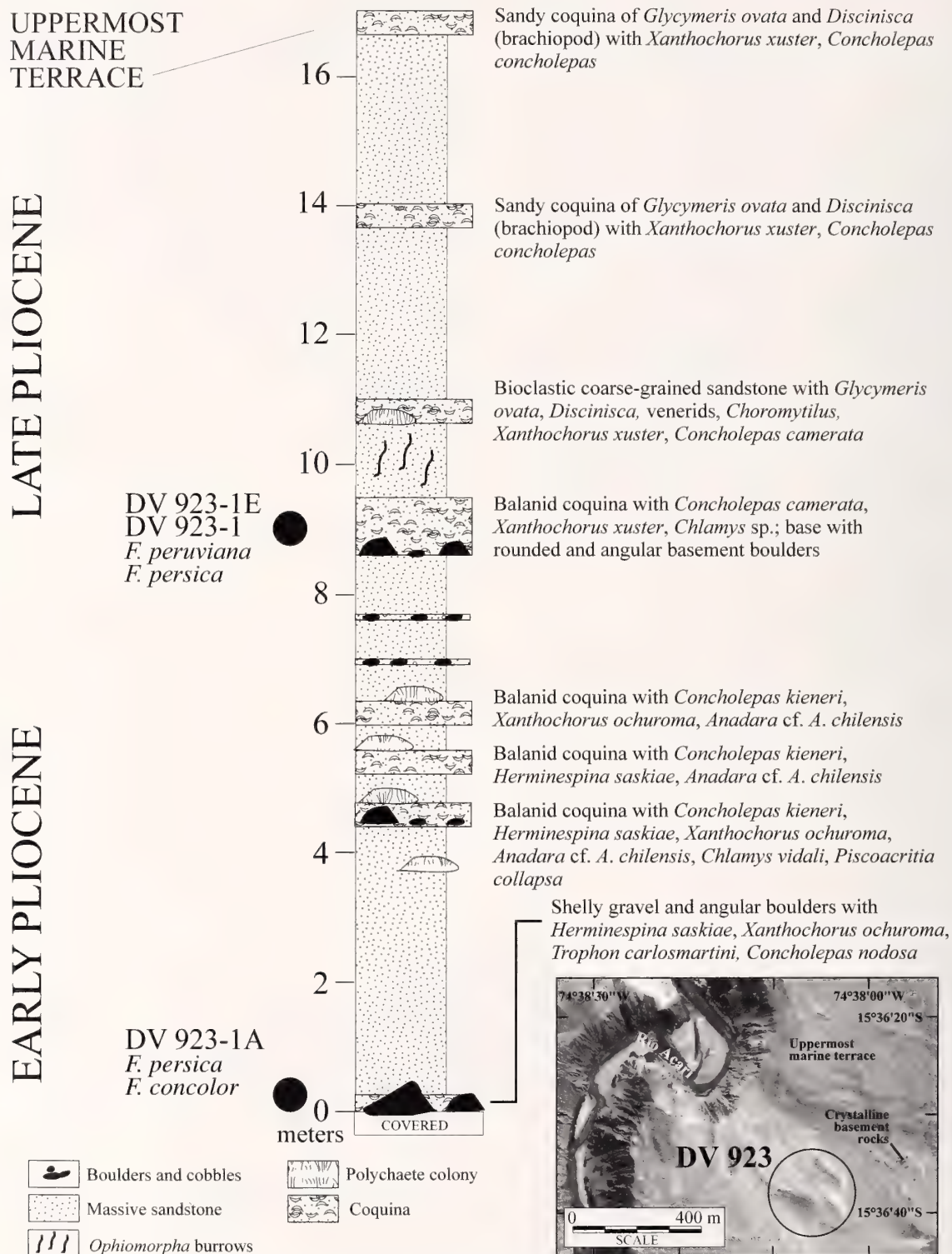


Figure 3. Lithologic section at the Acari site southeast of the Rio Acari, type locality (DV 923) for *Fissurella persica*, sp. nov. The location map is shown in inset. Associated mollusks listed in section are discussed in DeVries (2000, 2003, 2005a, 2005b), DeVries & Hess (2004), and DeVries & Vermeij (1997).

Fissurella (Fissurella) maxima Sowerby, 1835

Figures 4–10, 17, 18

Fissurella maxima Sowerby, 1835a, p. 123.*Fissurella maxima* Sowerby, 1835b, p. 3, fig. 18.*Fissurella maxima* Sowerby, 1835. McLean, 1984a, p. 25, figs. 51–63.*Fissurella maxima* Sowerby, 1835. Oliva & Castilla, 1992, p. 92, fig. 4.*Fissurella maxima* Sowerby. Alamo & Valdivieso, 1997, p. 7, fig. 12.*Fissurella maxima* Sowerby, 1835. Guzmán et al., 1998, p. 29, with figure.*Fissurella maxima* Sowerby, 1834 [sic]. Forcelli, 2000, p. 48, fig. 23.

Diagnosis: Shell large. Ribs strong, wide, well differentiated by size, corrugated to imbricate. Purplish rays broad. Margin coarsely crenulated. Rays penetrate entire calcitic layer.

Discussion: Small specimens with characters of *Fissurella maxima*, including coloration, were found in bioclastic sandstones in the upper part of the Huacallaco section (Figure 2) and assigned a late Pliocene age based on the presence of associated molluscan taxa [*Prisogaster valenciai* DeVries, 2006, *Acanthina unicornis*, *Chorus* transitional between *C. giganteus* (Lesson, 1830) and *C. grandis* (Philippi, 1887), *Concholepas camerata*, *Xanthochorus xuster* (DeVries 1997, 2000, 2003, 2005a, 2006)].

Two Peruvian specimens of *Fissurella maxima* exhibit oval external scars from the epibiotic limpet, *Scurria variabilis* (Sowerby, 1839) [= *Scurria parasitica* (Orbigny, 1841); see Espoz et al., 2004] (Figure 8). Such scars are most often found on Recent specimens of *F. crassa* and *F. limbata* (Figures 22, 35).

Material: MUSM INV 164, DV 401-1, Recent, L 44.4, W 30.9, H 10.1; MUSM INV 165, DV 1032-1, late Pliocene, L 37.6, W 27.5, H 7.7; UWBM 98437, Lomas, Recent, L 87.7, W 59.4, H 22.0; UWBM 98438, Lomas, L 75.9, W 48.7, H 17.5; UWBM 98439, Lomas, L 55.3, W 36.9, H 13.2; UWBM 98440, Lomas, L 51.6, W 31.7, H 10.6; UWBM 98441, DV 1372-1, Recent, L 60.3, W 35.8, H 13.7; UWBM 98442, DV 1372-1, L 65.7, W 42.8, H 14.7; UWBM 98443, DV 1628-6, late Pliocene, L 43.5, W 29.3, H 10.6; UWBM 98444, DV 1254-Ball0, late Pliocene, L 16.3, W 10.4, H 4.5; UWBM 98482, DV 1418-1, late Pliocene, L 32.6, W 21.5, H 5.3; UWBM 98483, DV 1418-1, L (12.6).

Occurrence: Late Pliocene: southern Peru. Pleistocene: central Chile. Recent: north-central Peru to central Chile.

Fissurella (Fissurella) concolor Philippi, 1887

Figures 11–16, 19

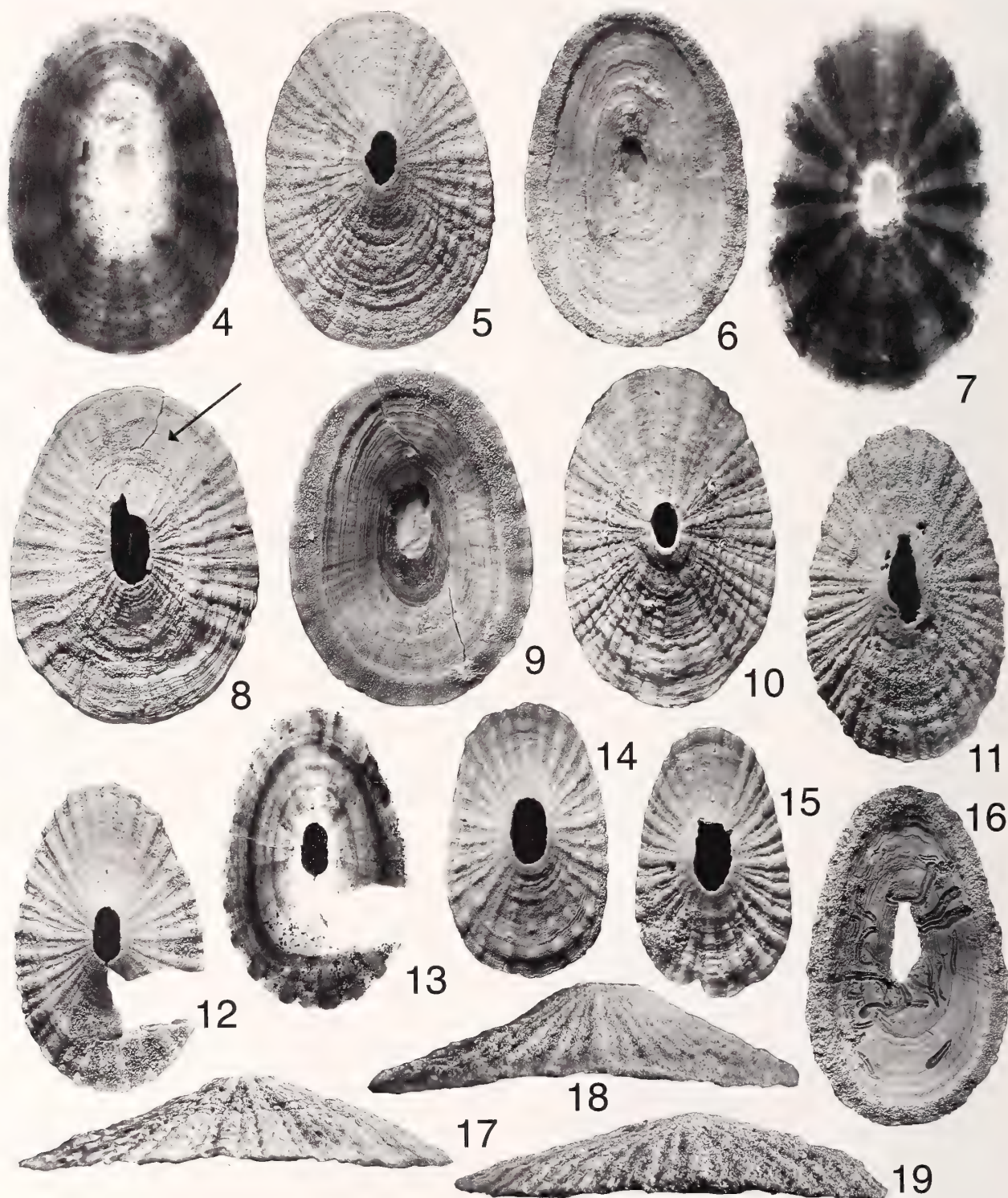
Fissurella concolor Philippi, 1887, p. 98, pl. 58, fig. 8.*Fissurella concolor* Philippi, 1887. McLean, 1984a, p. 15, fig. 17.

Diagnosis: Shell medium-sized, elongate, tapered. Ribs strong, well differentiated by size, weakly corrugate or smooth. Margin moderately wide, coarsely crenulated.

Description: Shell length up to 60 mm, elongate, strongly tapered anteriorly. Height low. Sides of shell elevated. Ribs prominent, sharply rounded, smooth to slightly imbricate, differentiated into primary ribs, some bifurcated, usually with three intervening secondary ribs, the medial being stronger; smaller specimens with one intervening secondary rib between primary ribs. Margin moderately wide, crenulated by ribs. Rays narrow, purplish, generally coinciding with primary ribs; anterior rays weak or absent. Aragonitic inner layer missing. Foramen anterior to center, shape unknown.

Discussion: *Fissurella concolor* was first described from Pliocene beds near Mejillones, Chile by Philippi (1887) and figured again by McLean (1984a). Peruvian specimens, like those from Chile, are elongate and have ribs that are more sharply raised and less imbricate than those on specimens of *F. maxima*. The oldest example from Peru came from the lowest boulder bed of the Acari locality (DV 923-1a) together with *F. persica*, sp. nov., and mollusks indicating an early Pliocene age [*Acanthina triangularis* DeVries, 2003, *Concholepas nodosa*, *C. kieneri*, and *Hermine spina saskiae* (DeVries, 1995, 2000, 2003; DeVries & Vermeij, 1997)]. Other specimens were found in the lowest cobble-rich bioclastic sandstone in the Huacallaco section (DV 1254-14); associated mollusks (*Acanthina* transitional between *A. triangularis* and *A. unicornis*; *Concholepas camerata*; *Xanthochorus xuster*) indicate an early late Pliocene age. Higher in the Huacallaco section the only strongly ribbed *Fissurella* specimens are referable to *F. maxima*.

Material: MUSM INV 171, DV 1032-2, early late Pliocene, L 35.9, W 22.1, H 7.0; MUSM INV 172, Huacallaco, early late Pliocene, L (26.2), W 16.9, H 5.9; MUSM INV 173, DV 1254-14, early late Pliocene, L 28.0, W 16.4, H 3.3; UWBM 98463, DV 923-1a, early Pliocene, L (11.1), W 9.1, H 2.0; UWBM 98464, Huacallaco, late Pliocene, L 47.9, W 29.1, H 10.8; UWBM 98465, DV 1032-2, L 24.5, W 14.5, H 5.2; UWBM 98466, DV 1032-2, L 19.6, W 16.9, H (5.1); UWBM 98467, DV 1254-6, late Pliocene, L 19.3, W



Figures 4-10, 17, 18. *Fissurella (Fissurella) maxima* Sowerby, 1835.

Figure 4. UWBm 98443, DV 1628-6. Late Pliocene. Transmitted light showing rays. Length is 43.5 mm.

Figure 5. UWBm 98443. Dorsal view.

Figure 6. UWBm 98443. Ventral view, aragonitic inner layer missing.

Figure 7. UWBm 98441, DV 1372-1. Recent. Transmitted light showing rays. Length is 60.3 mm.

11.5, H 4.1; UWB 98468, DV 1254-14, L 29.6, W 18.4, H 3.9; UWB 98469, DV 1254-14, L (37.9).

Occurrence: Early to early late Pliocene: southern Peru. Pliocene: north-central Chile.

Fissurella (Fissurella) aranea, sp. nov.

Figures 20, 21, 34

Diagnosis: Shell small, elongate-quadrate. Height low. Ribs sharply defined, alternating primary and secondary. Margin wide.

Description: Shell small, less than 30 mm long, elongate-quadrate, slightly tapered anteriorly. Height low. Ends slightly raised. Sculpture of well defined, closely spaced, narrow ribs, alternatingly primary and secondary; moderately imbricate at intersections with strong growth lines. No coloring preserved. Margin wide, irregularly scalloped. Foramen probably slightly anterior to center.

Discussion: Specimens of *Fissurella aranea* differ from contemporaneous small specimens of *F. persica*, sp. nov., by being more quadrate and having ribs that alternate regularly in size, in contrast with fine equally sized ribs on specimens of *F. persica*. Ribs on specimens of *F. concolor* and *F. maxima* are coarser and alternate less regularly.

Etymology: Latin noun 'aranea,' meaning 'spider net,' referring to the intersecting ribs and concentric growth lines on this species.

Type Locality: DV 1254, section along Panamerican Highway above Playa Huacilaco, 27 m in measured section (see Appendix).

Material: UWB 98479, DV 1254-Bal5, holotype, late early Pliocene; L 27.4, W 16.7, H (4.9); UWB 98480, DV 923-1e, early late Pliocene, L (17.9), W 13.2, H (2.7).

Occurrence: Late early Pliocene to early late Pliocene: southern Peru.

Fissurella (Fissurella) limbata Sowerby, 1835

Figures 22–33

Fissurella limbata Sowerby, 1835a, p. 123.

Fissurella limbata Sowerby, 1835b, p. 3, figs. 42, 66, 74.

Fissurella limbata Sowerby, 1835. McLean, 1984a, p. 55, figs. 212–224.

Fissurella limbata Sowerby, 1835. Oliva & Castilla, 1992, p. 7, fig. 10.

Fissurella limbata Sowerby. Alamo & Valdivieso, 1997, p. 93, fig. 10.

Fissurella limbata Sowerby, 1835. Guzmán et al., 1998, p. 28, with figure.

Fissurella limbata Sowerby, 1835. Forcelli, 2000, p. 49, fig. 25.

Diagnosis: Shell medium-sized. Ribs broad, subdued, some with weak secondary ribs; ribs often obsolete towards foramen. Margin wide. Calcitic outer layer with translucent veneer.

Discussion: Modern specimens of *Fissurella limbata* have ribs that are less well defined than those of *F. maxima*. Such specimens were encountered in bioclastic sandstones in the upper half of the Huacilaco section near Chala (DV 1254-14), together with specimens of *F. concolor*. One specimen (Figure 27) has a nearly full suite of primary, secondary, and tertiary ribs extending to the foramen, such as is seen on specimens of *F. maxima*, although the ribs are subdued and lack the imbricate texture of the latter species. Rays are seen to penetrate the entire calcitic outer layer, but perhaps only because the purple color of the flattened margin is faded.

Associated mollusks indicate a late Pliocene age. Not one Pliocene specimen exhibited the external scar of the epibiotic limpet, *Scurria variabilis*, which is commonly seen on modern specimens of *F. limbata* (Figures 22, 29).

Figure 8. MUSM INV 165, DV 1032-1. Late Pliocene. Dorsal view; arrow marks scar from *Scurria* limpet. Length is 37.6 mm.

Figure 9. MUSM INV 165, ventral view.

Figure 10. UWB 98440, Lomas. Recent. Dorsal view. Length is 51.6 mm.

Figure 17. UWB 98443, lateral view, anterior to right.

Figure 18. UWB 98441, lateral view, anterior to right.

Figures 11–16, 19. *Fissurella (Fissurella) concolor* Philippi, 1887.

Figure 11. UWB 98464, Huacilaco. Early late Pliocene. Dorsal view. Length is 47.9 mm.

Figure 12. MUSM INV 171, DV 1032-2. Late early Pliocene. Dorsal view. Length is 35.9 mm.

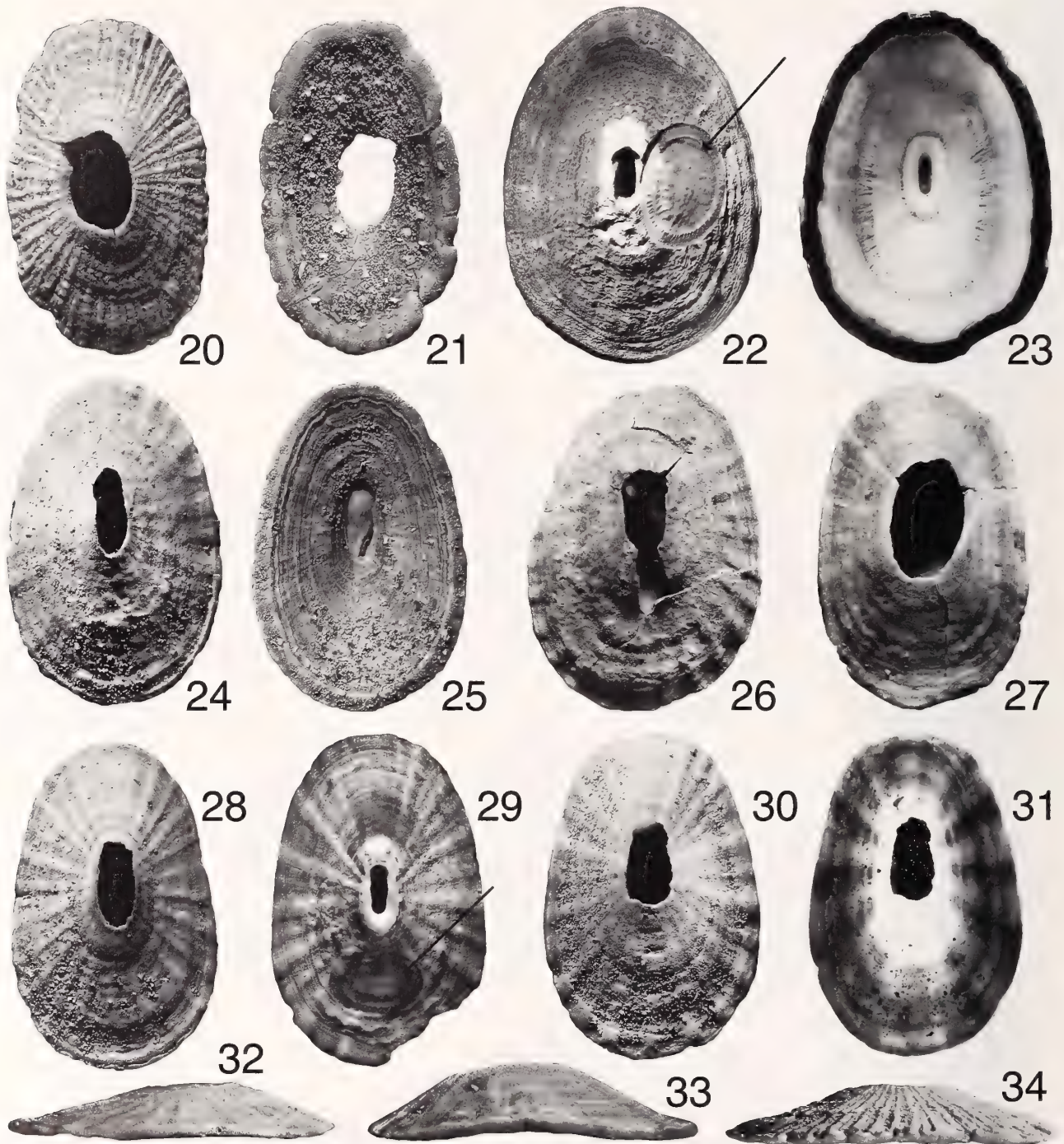
Figure 13. MUSM INV 171, transmitted light.

Figure 14. UWB 98465, DV 1032-2. Early late Pliocene. Dorsal view. Length is 24.5 mm.

Figure 15. MUSM INV 173, DV 1254-14. Early late Pliocene. Dorsal view. Length is 28.0 mm.

Figure 16. UWB 98464, ventral view.

Figure 19. UWB 98464, lateral view, anterior to right.



Figures 20, 21, 34. *Fissurella (Fissurella) aranea*, sp. nov. UWBM 98479, DV 1254-Bal5. Holotype. Late early Pliocene. Length is 27.4 mm.

Figure 20. Dorsal view.

Figure 21. Ventral view.

Figure 34. Lateral view, anterior to right.

Figures 22–33. *Fissurella (Fissurella) limbata* Sowerby, 1835.

Figure 22. MUSM INV 167, DV 810-1. Holocene. Dorsal view. Length is 60.8 mm. Arrow marks scar from *Scurria* limpet.

Figure 23. MUSM INV 167, ventral view.

Figure 24. MUSM INV 170, Hucallaco. Early late Pliocene. Dorsal view. Length is 37.6 mm.

Figure 25. MUSM INV 170, ventral view.

Material: MUSM INV 163, DV 1372-1, Recent, L 63.4, W 43.7, H 15.3; MUSM INV 167, DV 810-1, Holocene, L 60.8, W 43.6, H 18.7; MUSM INV 168, DV 1254-5, late Pliocene, L 62.8, W 42.1, H 17.0; MUSM INV 169, DV 1254-14, early late Pliocene, L (28.5); MUSM INV 170, lowest Huacllaco cobbles, 37 m, early late Pliocene, L 37.6, W 24.9, H 6.5; UWBM 98452, Lomas, Recent, L 50.4, W 33.7, H 12.9; UWBM 98453, Lomas, L 48.8, W 33.6, H 11.9; UWBM 98454, DV 810-1, L 72.2, W 49.8, H 18.8; UWBM 98455, DV 1254-6, late Pliocene, L 53.9, W 37.5, H (15); UWBM 98456, DV 1254-14, L 42.6, W 30.1, H 11.3; UWBM 98460, DV 1254-10, late Pliocene, L 36.4, W 24.4, H 8.2; UWBM 98461, DV 1254-14, L 34.6, W 21.9, H 6.2; UWBM 98462, DV 1254-14, L 36.6, W 23.9, H 8.7; UWBM 98457, DV 1372-1, L 36.9, W 23.9, H 9.0; UWBM 98458, DV 1372-1, L 38.6, W 25.9, H 8.9; UWBM 98459, DV 1372-1, L (22.9), W 16.8, H 7.0; UWBM 98478, DV 1254-2, early late Pliocene, L (27.7).

Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to Chiloé, Chile.

Fissurella (Fissurella) crassa Lamarck, 1822

Figures 35–37

- Fissurella crassa* Lamarck, 1822, 6(2), p. 11.
Fissurella crassa Lamarck, 1822. Sowerby, 1835b, p. 1, figs. 9, 11.
Fissurella crassa Lamarck, 1822. McLean, 1984a, p. 58, figs. 225–237.
Fissurella crassa Lamarck, 1822. Oliva & Castilla, 1992, p. 92, fig. 5.
Fissurella crassa Lamarck. Alamo & Valdivieso, 1997, p. 6, fig. 11.
Fissurella crassa Lamarck, 1822. Guzmán et al., 1998, p. 27, with figure.
Fissurella crassa Lamarck, 1822. Forcelli, 2000, p. 46, fig. 13.

Diagnosis: Shell medium-sized to large, elongate, with upturned ends and margins; margin with fimbriate edge. Ribs and rays poorly developed. Foramen elongate.

Discussion: Specimens of *Fissurella crassa* are more elongate and less tapered than those of *F. limbata* and have nearly obsolete ribs. A fragment of *Fissurella* from the lower half of the Huacllaco section (Figure 37) has the same uniquely scalloped, fimbriate, upturned margin as specimens of extant *F. crassa* and so is referred to this species.

Material: MUSM INV 166, DV 810-1, Holocene, L 61.1, W 36.3, H 13.3; UWBM 98447, DV 1372-1, Recent, L 63.6, W 35.9, H 14.7; UWBM 98448, Lomas, Recent, L 52.3, W 31.1, H 11.3; UWBM 98449, Lomas, L 42.6, W 24.1, H 9.6; UWBM 98450, DV 810-1, L 62.8, W 39.6, H 15.4; UWBM 98451, Huacllaco, 39 m, early late Pliocene, L (19.7).

Occurrence: Early late Pliocene: southern Peru. Late Pliocene: Chile. Recent: north-central Peru to Chiloé, Chile.

Fissurella (Fissurella) peruviana Lamarck, 1822

Figures 38–42

- Fissurella peruviana* Lamarck, 1822, p. 15.
Fissurella peruviana Lamarck, 1822. McLean, 1984a, p. 21, figs. 31–50.
Fissurella peruviana Lamarck, 1822. Alamo & Valdivieso, 1997, p. 7, fig. 13.
Fissurella peruviana Lamarck, 1822. Guzmán et al., 1998, p. 29, with figure.
Fissurella peruviana Lamarck, 1822. Forcelli, 2000, p. 48, fig. 22.

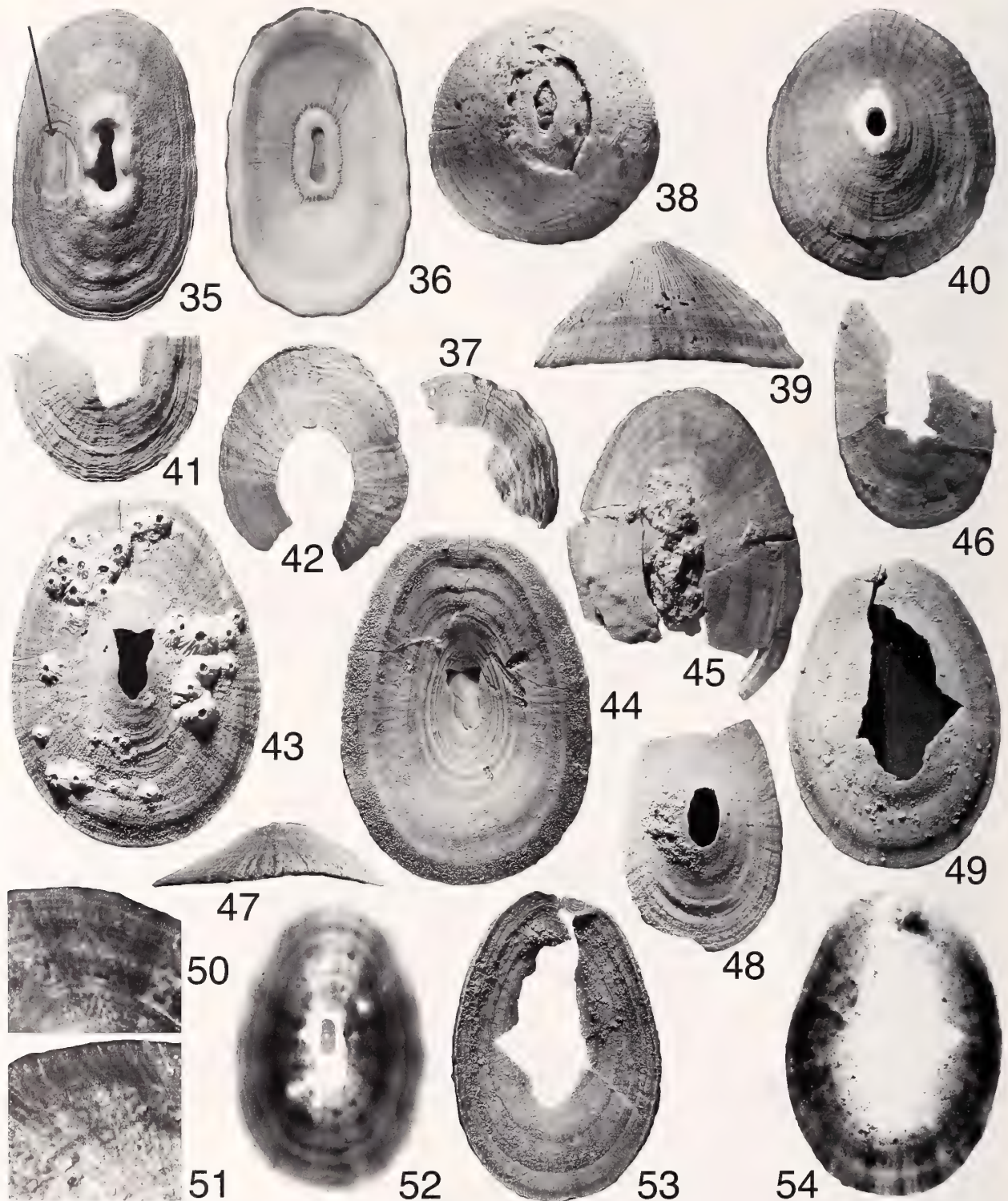
Diagnosis: Shell small, profile high. Fine primary and secondary ribs. Color usually charcoal gray; rays obscured. Margin narrow. Foramen small, oval.

Discussion: Specimens with the high conic shell and fine ribs of *Fissurella peruviana* were found in a coquina bed nine meters above the valley floor of the Acari outcrop (Figure 3). Associated mollusks (*Concholepas camerata*, *Xanthochorus xuster*, *Stramonita chocolata*) indicate a late Pliocene age (DeVries, 2000, 2005a, 2007).

A specimen (OSU 38157) assigned herein to *Fissurella peruviana* was found in the gravel-rich cross-bedded sandstones of the basal Taime Formation in northern Peru (DV 239-11; DeVries, 1986, 1988).

←

- Figure 26. UWBM 98456, DV 1254-14. Early late Pliocene. Dorsal view. Length is 42.6 mm.
 Figure 27. UWBM 98462, DV 1254-14. Dorsal view. Length is 36.6 mm.
 Figure 28. UWBM 98461, DV 1254-14. Dorsal view. Length is 34.6 mm.
 Figure 29. UWBM 98457, DV 1372-1. Recent. Dorsal view. Length is 36.9 mm. Arrow marks scar from *Scurria* limpet.
 Figure 30. UWBM 98460, DV 1254-10. Late Pliocene. Dorsal view. Length is 36.4 mm.
 Figure 31. UWBM 98460, transmitted light showing rays.
 Figure 32. UWBM 98461, lateral view, anterior is to right.
 Figure 33. UWBM 98462, lateral view, anterior is to left.



Figures 35–37. *Fissurella (Fissurella) crassa* Lamarck, 1822.

Figure 35. MUSM INV 166, DV 810-1. Holocene. Dorsal view. Length is 61.1 mm. Arrow marks scar from *Scurria* limpet.

Figure 36. MUSM INV 166, ventral view.

Figure 37. UWB 98451, Huacilaco. Early late Pliocene. Dorsal view of fragment. Length is 19.7 mm.

Figures 38–42. *Fissurella (Fissurella) peruviana* Lamarck, 1822.

The elongate foramen differs from the oval foramen seen on southern Peruvian and Chilean specimens (Figure 38) but the size and arrangement of radial ribs are identical, as is the high conic profile.

Material: MUSM INV 161, DV 923-1e, early late Pliocene, L (25.3); MUSM INV 162, DV 923-1, early late Pliocene, L (26.0), W 21.5, H (7.4); OSU 38157, DV 239-11, late Pliocene, L 21.4, W 20.7, H 10.8; UWBM 98424, DV 1141-1, Recent, L 40.3, W 34.2, H 16.5; UWBM 98425, DV 1141-1, L 33.4, W 23.9, H 15.4; UWBM 98426, La Mina, Recent, L 33.4, W 24.9, H 12.6; UWBM 98427, DV 599-2, middle Pleistocene, L 31.0, W 22.5, H 10.2; UWBM 98428, DV 1141-1, L 19.9, W 13.8, H 9.3; UWBM 98429, DV 401-1, Recent, lot of 2; UWBM 98430, DV 923-1e, early late Pliocene, L (20.6), W 25.3, H 10.4.

Occurrence: Early late Pliocene: northern to southern Peru. Recent: north-central Peru to south-central Chile.

Fissurella (Fissurella) latimarginata Sowerby, 1835

Figures 43, 44, 47, 48

Fissurella latimarginata Sowerby, 1835a, p. 126.

Fissurella latimarginata Sowerby, 1835b, p. 3, fig. 69.

Fissurella latimarginata Sowerby, 1835. McLean, 1984a, p. 28, figs. 64–79.

Fissurella latimarginata Sowerby, 1835. Oliva & Castilla, 1992, p. 92, fig. 6.

Fissurella latimarginata Sowerby. Alamo & Valdivieso, 1997, p. 6.

Fissurella latimarginata Sowerby, 1835. Guzmán et al., 1998, p. 28, with figure.

Fissurella latimarginata Sowerby, 1835. Forcelli, 1835, p. 46, fig. 12.

Diagnosis: Shell large, height low to moderate. Color charcoal gray. Ribs fine, poorly differentiated; rays usually obscured. Margin wide. Foramen elongate.

Discussion: A specimen of *Fissurella latimarginata* (Figure 43) was found in the upper part of Unit III of the Huacllaco section (Figure 2), together with the transitional *Chorus giganteus*/*C. grandis* and *Concholepas camerata*, both indicative of a late Pliocene age. Another specimen of *F. latimarginata* was found at Quebrada Champeque (DV 1251-1), 10 m above basement rocks and 10 m below the uppermost marine terrace, together with *Concholepas camerata*, *Xanthochorus xuster*, and *Acanthina unicornis*, which collectively indicate a late Pliocene age (DeVries, 2000, 2003, 2005a).

Material: MUSM INV 163, DV 1251-1, late Pliocene, L (27.9), 19.2, H 7.8; UWBM 98433, DV 1032-1, late Pliocene, L 49.5, W 35.6, H 9.1; UWBM 98434, DV 1372-1, Recent, L 55.6, W 37.2, H 13.2; UWBM 98435, Lomas, Recent, L 69.5, W 50.2, H 16.4; UWBM 98436, Lomas, 53.5, W 37.5, H 11.8.

Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to central Chile.

Fissurella cumingi Reeve, 1849

Fissurella cumingi Reeve, 1849, pl. 3, fig. 17.

Fissurella cumingi Reeve, 1849. Hupé, 1854, p. 238.

Fissurella cumingi Reeve, 1849. McLean, 1984a, p. 31, figs. 80–94.

Fissurella cumingi Reeve, 1849. Oliva & Castilla, 1992, p. 92, fig. 7.

Fissurella cumingi Reeve, 1849. Guzmán et al., 1998, p. 27, with figure.

←

Figure 38. OSU 38157, DV 239-11. Late Pliocene. Dorsal view. Length is 21.4 mm.

Figure 39. UWBM 98424, DV 1141-1. Recent. Dorsal view. Length is 40.3 mm.

Figure 40. UWBM 98424, lateral view, anterior is to left.

Figure 41. UWBM 98430, DV 923-1e. Early late Pliocene. Dorsal view of fragment. Length is 20.6 mm.

Figure 42. MUSM INV 162, DV 923-1. Early late Pliocene. Dorsal view of fragment. Length is 26.0 mm.

Figures 43, 44, 47, 48. *Fissurella (Fissurella) latimarginata* Sowerby, 1835.

Figure 43. UWBM 98433, DV 1032-1. Late Pliocene. Dorsal view. Length is 49.5 mm.

Figure 44. UWBM 98433, ventral view.

Figure 47. MUSM INV 163, DV 1251-1. Late Pliocene. Dorsal view. Length is 27.9 mm.

Figure 48. MUSM INV 163, lateral view, anterior is to right.

Figures 45, 46. *Fissurella (Fissurella) persica* sp. nov.

Figure 45. UWBM 98470, DV 923-1a, holotype. Early Pliocene. Dorsal view. Length is 31.9 mm.

Figure 46. UWBM 98477, DV 1254-Bal5. Late early Pliocene. Dorsal view. Length is 20.5 mm.

Figures 49–54. *Fissurella (Fissurella) pulchra* Sowerby, 1835.

Figure 49. UWBM 98432, DV 1251-1. Late Pliocene. Dorsal view. Length is 52.6 mm.

Figure 50. LACM 75-31 a, Chile. Recent. Close-up showing unique mottling.

Figure 51. UWBM 98432, close-up showing unique mottling.

Figure 52. LACM 75-31 b, Chile. Recent. Transmitted light showing acicular rays.

Figure 53. UWBM 98432, ventral view.

Figure 54. UWBM 98432, transmitted light showing acicular rays.

Fissurella cumingi Reeve, 1849. Forcelli, 2000, p. 48, fig. 24.

Diagnosis: Shell large, light colored, with fine ribs and well-defined rays.

Discussion: A large broken and worn specimen of *Fissurella cumingi* was found on a middle Pleistocene terrace (elevation 160 m above sea level) north of Chala. A large modern specimen from Lomas is very similar to the Pleistocene specimen.

Material: LACM 75-32, Chile, Recent, lot of 31; UWBm 98445, DV 465-1, middle Pleistocene, L (59.3), W 55.0, H 20.3; UWBm 98446, Lomas, Recent, L 77.3, W 55.7, H 25.3.

Occurrence: Early middle Pleistocene: southern Peru. Recent: southern Peru to south-central Chile.

Fissurella (Fissurella) persica, sp. nov.

Figures 45, 46

Diagnosis: Shell small, height low. Ribs fine, weak, generally undifferentiated. Rays broad, forming a suffusion of purple-peach color in transmitted light.

Description: Shell small, length less than 40 mm. Oval, sharply tapered anteriorly. Height low. Calcitic outer layer thin. Sculpture of numerous thin ribs; ribs equally sized, barely raised, differentiated in anterior quadrant only. Ground color cream; broad rays of purplish-peach color. Margin flat, narrow, coloring of rays passes through entire thickness of outer layer. Foramen not preserved, probably just anterior to center.

Discussion: Specimens of *Fissurella persica* closely resemble those of the opaquely gray *F. latimarginata* with their fine ribs and sharply tapered anterior. They are lighter colored, however, like specimens of *F. cumingi*, with visible rays and a narrow margin. Their ribs are more uniformly sized than those of both *F. latimarginata* and *F. cumingi*.

The holotype of *Fissurella persica* was found in bioclastic gravel near the base of the Acarí outcrop (Figure 3). Its occurrence with *Trophon carlosmartini*, *Hermespina saskiae*, and *Xanthochorus ochuroma* indicates an early Pliocene age. Fragments of *F. persica* were also found in the upper bioclastic sandstones of the Acarí locality (early late Pliocene) and Unit I of the Huacallaco outcrop (late early Pliocene).

Etymology: Latin noun '*persica*,' meaning 'peach,' for the purple-peach color of the species' rays under transmitted light.

Type Locality: DV 923, knobs southeast of the Río Acarí, east of Chauviña (Figure 3; see Appendix).

Material: MUSM INV 174, DV 923-1, early late Pliocene, L (12.9); MUSM INV 175, DV 923-1, L (17.5); UWBm 98431, DV 923-1, early late Pliocene, L (21.8); UWBm 98470, DV 923-1a, early Pliocene, holotype, L (31.9), W 25.0, H 7.2; UWBm 98471, DV 1254-Bal5, late early Pliocene, L (25.4); UWBm 98472, DV 923-1e, early late Pliocene, L (27.3); UWBm 98473, DV 923-1e, L (29.5); UWBm 98476, DV 1254-2, early late Pliocene, L 22.7, W 15.4, H 2.8; UWBm 98477, DV 1254-Bal5, (20.5), W 14.4, H 3.4.

Occurrence: Early to early late Pliocene: southern Peru.

Fissurella (Fissurella) pulchra Sowerby, 1835

Figures 49–54

Fissurella pulchra Sowerby, 1835a, p. 124.

Fissurella pulchra Sowerby, 1835b, p. 3, fig. 24.

Fissurella pulchra Sowerby, 1835. McLean, 1984a, p. 63, figs. 254–267.

Fissurella pulchra Sowerby, 1835. Oliva & Castilla, 1992, p. 93, fig. 11.

Fissurella pulchra Sowerby, 1835. Guzmán et al., 1998, p. 30, with figure.

Fissurella pulchra Sowerby, 1835. Forcelli, 2000, p. 49, fig. 27.

Diagnosis: Shell medium-sized, smooth. Height very low. Surface with purple-and-white streaky mottling. Broad rays superimposed on irregularly spaced acicular rays.

Discussion: A single specimen of *Fissurella pulchra*, distinguished by its exterior mottling and smooth surface, was discovered in late Pliocene deposits north of Chala. Both modern and fossil examples have weakly developed ribs anteriorly.

Material: LACM 75-31, Recent, Chile, lot of 10; UWBm 98432, DV 1251-1, L 52.6, W 36.0, H 8.4.

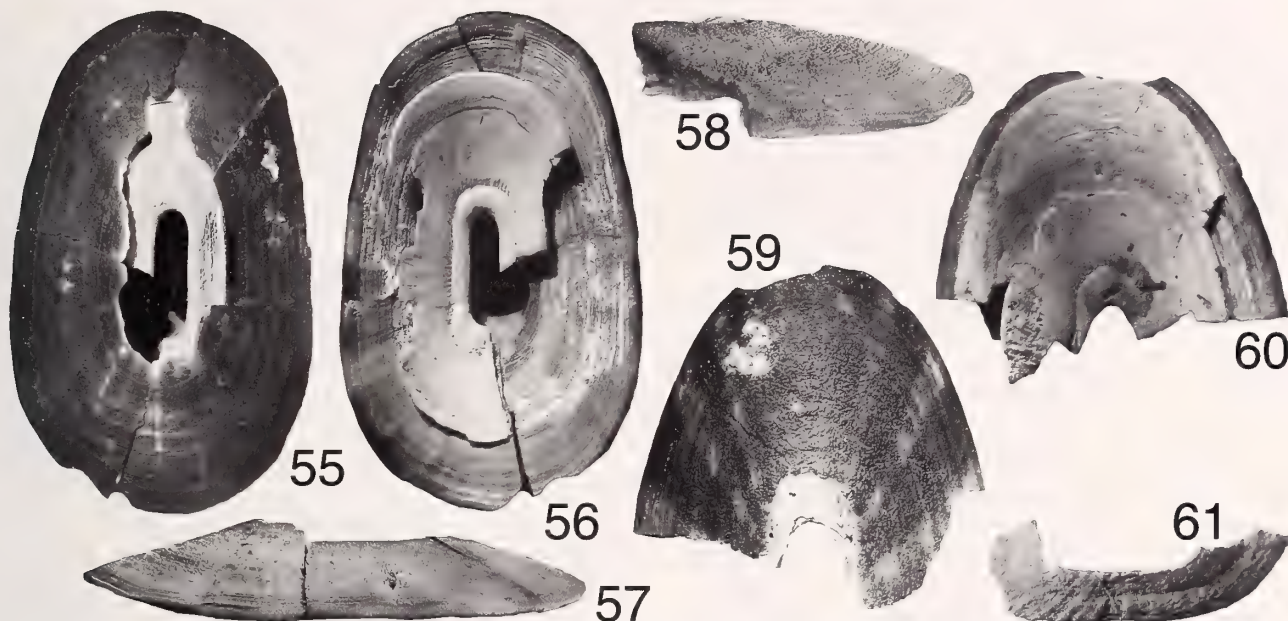
Occurrence: Late Pliocene: southern Peru. Recent: north-central Peru to central Chile.

Fissurella (Fissurella) mcleani, sp. nov.

Figures 55–57

Diagnosis: Shell medium-sized, elongate. Exterior black, smooth. Foramen exceptionally elongate. Ends elevated.

Description: Shell medium-sized, length almost 60 mm, elongate, tapered slightly anteriorly; ends of shell elevated. Height low. Surface black, smooth, with rare radial wrinkles marking edges of obsolete radial ribs. Numerous thin reddish rays, only visible, barely,



Figures 55–57. *Fissurella (Fissurella) mcleani*, sp. nov. UWB 98475, DV 1635-2. Holotype. Early Pliocene. Length is 58.4 mm.

Figure 55. Dorsal view.

Figure 56. Ventral view showing partial layer of aragonite and very elongate foramen.

Figure 57. Lateral view, anterior to right.

Figures 58–60. *Fissurella (Fissurella) geoglypha*, sp. nov. UWB 98474, Yauca. Holotype. Early Pliocene. Length is 35.0 mm.

Figure 58. Lateral view, anterior to right.

Figure 59. Dorsal view.

Figure 60. Ventral view, showing partial layer of aragonite.

Figure 61. *Diodora* sp. UWB 98481, DV 923-1a. Early Pliocene. Dorsal view of fragment; note squared off posterior to left.

Length is 18.4 mm.

apically. Margin moderately wide, smooth, with broad obsolete rays producing alternating cream and black-colored intervals. Aragonite layer partially preserved. Foramen situated slightly posteriorly; exceptionally elongate, without constrictions.

Discussion: *Fissurella (Fissurella) mcleani* has an exceptionally elongate foramen and a smooth black surface. Specimens of *Fissurella pulchra* are equally smooth, but possess a normally elongate foramen and lack the deep black color of *F. mcleani*.

Associated mollusks from the same beds (*Anadara* cf. *A. chilensis*, *Acanthina obesa* DeVries, 2003, *Concholepas kieneri*, *Hermiespina saskiae*, *Xanthochorus ochur-oma*) at locality DV 1635-1 indicate an early Pliocene age; the presence of *X. eripepomus* DeVries, 2005, further suggests a late early Pliocene age.

Etymology: Named in recognition of James H. McLean (Natural History Museum of Los Angeles County) and his studies on *Fissurella (Fissurella)*.

Type Locality: DV 1635, Yauca depression, west of Panamerican Highway, northwest of Yauca (Figure 62; see Appendix).

Material: UWB 98475, DV 1635-2, holotype, late early Pliocene, L 58.4, W 32.6, H 13.3.

Occurrence: Late early Pliocene: southern Peru.

Fissurella (Fissurella) geoglypha, sp. nov.

Figures 58–60

Diagnosis: Shell medium-sized, smooth. Exterior black; cream-colored rays sharply defined, broad.

Description: Shell with estimated length of 60 mm, anterior strongly tapered, posterior unknown. Height low. Anterior end of shell elevated. Exterior smooth. Rays sharply defined, broad, penetrate calcitic outer layer. Margin rounded, moderately wide. Aragonitic shell layer partially preserved.

Discussion: The holotype of *Fissurella geoglypha* is more bowed than the smooth flat specimens of *F. pulchra* and lacks the latter's characteristic mottling; it is also less quadrate than the holotype of *F. mcleani*, which lacks any broad rays. Associated mollusks from the Yauca roadcut (*Anadara* cf. *A. chilensis*, *Concho-*

lepas nodosa, *Xanthochorus ochuroma*) indicate an early Pliocene age (DeVries, 2000, 2005a).

Etymology: Named for radiating geoglyphs that are part of the pre-Columbian Nazca lines in southern Peru.

Type Locality: Yauca, roadcut in Panamerican Highway on north side of Río Yauca (Figure 62; see Appendix).

Material: UWBM 98475, Yauca, holotype, late early Pliocene, L (35.0), W (36.5), H 12.1.

Occurrence: Late early Pliocene: southern Peru.

DISCUSSION

There is no consensus regarding the grouping of related species within *Fissurella* (*Fissurella*). Pilsbry (1890) recognized four species groups based on shell morphology, whereas McLean (1984a) defined three groups according to the relative thickness of the aragonitic inner and calcitic outer layers. Stuber (1991) utilized 34 anatomical, radular, and morphological characters to produce a cladogram for 26 extinct and extant fissurellid taxa. She recognized a primitive clade comprising *F. peruviana* and the two extralimital northern hemisphere species (*F. nimbosea*, *F. volcano*), a polytomous clade that included South American and South African species with well developed ribs, and a clade with smooth-shelled, weakly ribbed, and finely ribbed taxa.

The ensuing description of new morphological groups of *Fissurella* (*Fissurella*) is informed by a consideration of species' temporal ranges but is based largely on shell sculpture. These new groups are compared with clades derived from an analysis of molecular data by Olivares (2006).

Groups of related *Fissurella* (*Fissurella*) species

Coarsely ribbed group: *Fissurella maxima*, *F. costata*, and *F. picta* have long been considered closely related because of their similar coarse radial sculpture (Pilsbry, 1890; McLean, 1984a; Stuber, 1991). All three species occur in Pleistocene deposits of Chile (Herm, 1969); *F. picta* is also found on Pleistocene marine terraces in Argentina (Aguirre et al., 2005). Of the three taxa, the only Peruvian species, *F. maxima*, occurs in the upper part of Unit III at Huacallaco (Figure 2), but not in *Fissurella*-bearing beds of Unit II or the lower part of Unit III, suggesting that the species may have first appeared following the early late Pliocene. Other coarsely ribbed species (*F. concolor*, *F. aranea*) extend the record of this group back to the early Pliocene.

'limbata' lineage: Specimens of *Fissurella limbata* have low, broad, and sometimes obsolete ribs and few

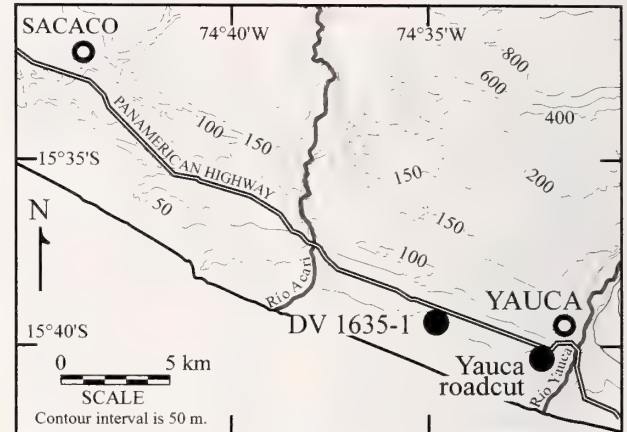


Figure 62. Type localities of *Fissurella mcleani*, sp. nov. (DV 1635-1) and *F. geoglypha*, sp. nov. (Yauca roadcut).

secondary ribs. The oldest examples are found in upper Unit II beds at Huacallaco. Some Huacallaco specimens have ribs nearly as well differentiated as those on specimens of late Pliocene *F. maxima* (compare Figure 28 with Figure 8), suggesting that *F. limbata* diverged from the coarsely ribbed group during the late early Pliocene.

Finely ribbed group: The fossil record of *F. latimarginata* (late Pliocene to Recent) and *F. persica* (early Pliocene) shows that finely ribbed species have long constituted a distinct morphological group. *Fissurella peruviana*, another species with fine ribs, appeared first during the early late Pliocene (Figure 3), suggesting it is more deeply rooted within the group than *F. latimarginata*. Less deeply rooted may be *F. cumingi*, an extant species greatly resembling *F. latimarginata* that was found on an early middle Pleistocene marine terrace.

Smooth-shelled group: A single specimen of *Fissurella pulchra* (Figure 49) was found in upper Pliocene deposits of southern Peru. The discovery of two new late early Pliocene smooth-shelled species, *F. mcleani* (Figure 55) and *F. geoglypha* (Figure 59), shows that this group was well established as early as the other morphological groups.

'crassa' lineage: The fimbriate wrinkle-ribbed *Fissurella crassa* occurs in early late Pliocene deposits of southern Peru (Figure 2), as well as Pliocene beds in Chile (McLean, 1984a). Its unusual blunt anterior and weakly developed and widely spaced primary ribs crossing an otherwise smooth surface makes its assignment to other groups problematic.

Unassigned taxa: Some species of *Fissurella* (*Fissurella*) are difficult to assign to an existing morphological group. *Fissurella radiosa* Lesson, 1831, a late Pleistocene to Recent species from southern Chile and Argentina, might be placed with finely ribbed taxa, although its narrow ribs are sharply elevated. The

extant *F. bridgesii* Reeve, 1849, from Peru and Chile, is irregularly striated and ribbed and might belong with finely ribbed taxa. *F. nigra* Lesson, 1831, a large extant species from southern Chile, has fine striations and is not clearly a member of any group.

To summarize: data from western South America point to the existence of at least five fissurellid groups with fossil and modern constituents (Figure 63): a coarsely ribbed group (*F. aranea*, *F. concolor*, *F. maxima*, *F. picta*, *F. costata*), a 'limbata' lineage (*F. limbata*), a finely ribbed group (*F. persica*, *F. peruviana*, *F. latimarginata*, *F. cumingi*, *F. oriens* Sowerby, 1835, *F. bridgesii*), a 'crassa' lineage (*F. crassa*), and a smooth-shelled group (*F. mcleani*, *F. geoglyphia*, *F. pulchra*). The differentiated ribs on some fossil specimens of *F. limbata* suggest the 'limbata' lineage and the coarsely ribbed group (*F. maxima* and others) share a common early Pliocene ancestor. All morphological groups were already established by the late early Pliocene, implying their common ancestor probably existed no more recently than the earliest Pliocene. To date, however, *Fissurella* of such antiquity have not been found in southern Peru.

Comparison with Molecular Data

Olivares (2006) sequenced partial nucleotide sequences of several mitochondrial and nuclear genes from all 13 of McLean's (1984a) extant South American species of *Fissurella* (*Fissurella*), as well as the extant Caribbean *F. nimbosea* and extant eastern Atlantic *F. schrammi* and *Diodora graeca* (Linnaeus, 1758). His molecular phylogeny, which is remarkably congruent with the phylogeny hinted at by the paleontological data, includes:

- a coarsely ribbed clade that includes *F. maxima* + *F. limbata*,
- a deeply rooted clade with finely ribbed taxa, including *F. latimarginata* + *F. cumingi*, and a sister group composed of *F. pulchra* + *F. radiosa*,
- a deeply rooted *F. peruviana* that is a sister taxon to other finely ribbed species, and
- a deeply rooted *F. crassa* with uncertain clade affinities.

The most significant incongruity between the molecular and morphological species groupings is the placement of *Fissurella radiosa*. That the broad, low, smooth-shelled *F. pulchra* and elongate, high-crowned, sharply ribbed *F. radiosa* could be sister species (Olivares, 2006) is startling. Yet, every tree-producing algorithm presented Olivares with the same *pulchra* + *radiosa* group, no matter which DNA sequence was used. In the case of randomly amplified polymorphic DNA (RAPD) data analyzed using the UPGMA method (unweighted pair group method with arithmetic

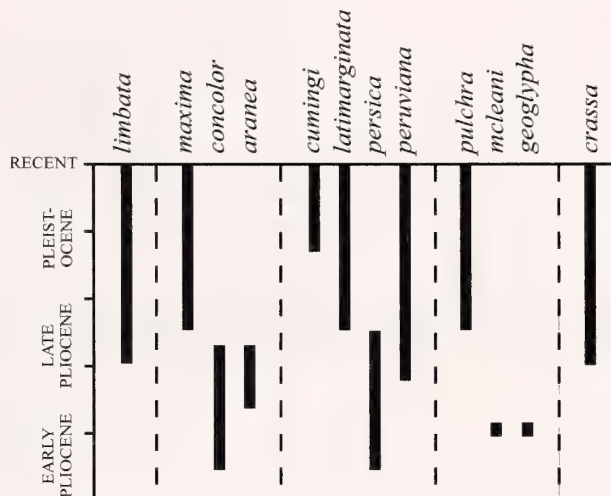


Figure 63. Estimates of temporal ranges for species of *Fissurella* (*Fissurella*) found in southern Peru.

tic mean), however, *F. radiosa* was grouped with *F. crassa* and *F. nigra* in a deeply rooted clade (Olivares, 2006). The discrepant phylogenetic results for *F. radiosa* remain unexplained.

Molecular ages for branching within the *Fissurella* (*Fissurella*) clade of Olivares (2006) are consistently younger compared with ages inferred from paleontological data (Table I). The discrepancies may be due in part to an age estimate for the uppermost terrace in southern Peru (2 Ma) that is too old or molecular calibration points that are too young (e.g., Pleistocene ages for the first appearance of *F. maxima* and *F. peruviana*).

Diversity Patterns

The species richness of Chilean and Peruvian fissurellid faunas for the Pliocene and Quaternary is summarized in Table II. Species richness appears to have increased during the Quaternary, a trend contrary to that for the rest of the Peruvian molluscan fauna (DeVries, 1995, 1997, 2001, 2003). Alternatively, fissurellids may simply be poorly preserved in older deposits. Extinct species of *Fissurella* are found only in Pliocene beds, not in Pleistocene deposits, in agreement with diversity patterns for the entire Pliocene-Quaternary molluscan fauna of western South America, which suffered a major species-level extinction during the late Pliocene (Herm, 1969; DeVries, 1985, 2001; Rivadeneira & Marquet, 2007).

Large species of *Fissurella* (>80 mm maximum length) appear only in Quaternary deposits (Table III). In contrast, the oldest species of *Fissurella* (*F. aranea*, *F. persica*) are among the smallest species (maximum length < 40 mm).

Origin of South American *Fissurella*

Fissurella (*Fissurella*) is notable for its taxonomic diversity in western South America since the early Pliocene and complete lack of a fossil record beforehand, even though upper Miocene littoral deposits are common in southern Peru (DeVries, 1998). Miocene Fissurellidae have been identified in Chile (Tavera, 1979; Nielsen, 2003), but the two new taxa illustrated by Nielsen (2003) are probably examples of *Diodora* Gray, 1821. The holotype of *Fissurella alternula* Tavera, 1979, might also be a *Diodora* (Tavera, 1979, 1991); other early Miocene species of *Diodora* are known from Chile (Nielsen, 2003) and an early Pliocene specimen has been found in southern Peru (Figure 61). South American *Fissurella* (*Fissurella*) most likely did not originate from early Miocene Chilean limpets.

If *Fissurella* was introduced to western South America, the avenues for introduction were few: immigration from (1) the Caribbean Sea or eastern North Pacific Ocean by way of northwestern South America, (2) the western Pacific Ocean or Indian Ocean by means of the high latitude West Wind Drift or equatorial countercurrents, or (3) the South Atlantic Ocean. Plausible examples exist for the first two scenarios, e.g., (1) the muricid, *Pterorytis* Conrad, 1862, arriving in southern Peru from the North Pacific Ocean during the early late Pliocene (DeVries, 2005c), and (2) the turbinid ancestor of *Prisogaster* Mörch, 1850, arriving from the western Pacific Ocean during the middle to late Miocene (DeVries, 2006). No persuasive examples of the third scenario are known (Nielsen, personal communication, 2007).

The occurrence of *Fissurella peruviana* in the Taime Formation of northern Peru (DeVries, 1986, 1988) could be construed as evidence for a Pliocene connection with northern hemisphere fissurellids (*F. nimbosa*, *F. volcano*) involving either emigration of Caribbean fissurellids southward (Olivares, 2006) or Peruvian taxa northward (Stuber, 1991). The anomalous presence of other higher latitude species in the

Table I

Ages for cladogenetic events affecting *Fissurella* (*Fissurella*). See Olivares (2006) for molecular data and basis for estimating ages. Paleontological ages are estimates based on faunal correlations with a radiometrically dated section at Sacaco (Muizon & DeVries, 1985) that also yielded biostratigraphically useful diatoms (H. Schrader, written communication, 1986) and a 2-Ma age for the uppermost uplifted marine terrace in southern Peru.

Event	Molecular age (Ma)	Paleontological age (Ma)
Basal polytomy for <i>Fissurella</i> (<i>Fissurella</i>)	3.5–2.14	>4
Divergence of <i>F. limbata</i> and ancestor of <i>F. maxima</i>	2.18–1.3	>2.3
<i>Fissurella latimarginata</i> species complex polytomy, including divergence of <i>F. latimarginata</i> and <i>F. cumingi</i>	0.2–0.12	>1.4

Taime Formation, however, suggests that a northward expansion of the Peruvian Faunal Province during the late Pliocene (DeVries, 1986) would best explain the odd occurrence of *F. peruviana* near the Equator. No other species of *Fissurella* (*Fissurella*) have been found in Miocene or Pliocene beds in northern Peru or Ecuador (e.g., Olsson, 1932, 1964; Pilsbry & Olsson, 1941; Marks, 1951; DeVries, 1986). Absent such a record, passage of diverse *Fissurella* populations during the Pliocene through northwestern South America from the Caribbean seems unlikely. The emigration of *Fissurella* from Peru to California, however, resulting

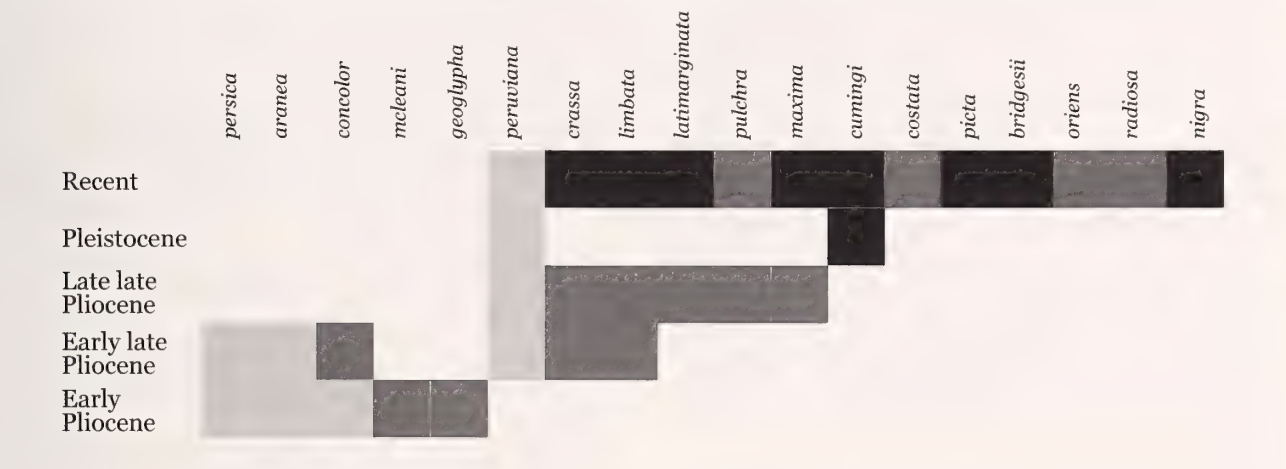
Table II

Species numbers of western South American *Fissurella* (*Fissurella*) for different time intervals since the early Pliocene. Data from Herm (1969), McLean (1984) and this report.

Time interval	Species list for Chile, Peru	Number of species
Recent	<i>bridgesii</i> , <i>costata</i> , <i>crassa</i> , <i>cumingi</i> , <i>latimarginata</i> , <i>limbata</i> , <i>maxima</i> , <i>nigra</i> , <i>oriens</i> , <i>peruviana</i> , <i>picta</i> , <i>pulchra</i> , <i>radiosa</i>	13
Pleistocene	<i>costata</i> , <i>crassa</i> , <i>cumingi</i> , <i>latimarginata</i> , <i>limbata</i> , <i>maxima</i> , <i>peruviana</i> , <i>picta</i> , <i>pulchra</i>	9
Late late Pliocene	<i>crassa</i> , <i>latimarginata</i> , <i>limbata</i> , <i>maxima</i> , <i>peruviana</i> , <i>pulchra</i>	6
Early late Pliocene	<i>concolor</i> , <i>crassa</i> , <i>limbata</i> , <i>persica</i> , <i>peruviana</i>	5
Early Pliocene	<i>arana</i> , <i>concolor</i> , <i>geoglyphia</i> , <i>mcleani</i> , <i>persica</i>	5

Table III

Maximum of sizes of *Fissurella* (*Fissurella*) species through time. Data from McLean (1984) and fossils described in this paper. Large species (maximum length > 80 mm) are shaded black; medium sized species (maximum length 40–80 mm) are shaded medium gray; and small species (maximum length < 40 mm) are shaded light gray.



in the Pleistocene establishment (Grant & Gale, 1931) of a single species, *F. volcano*, as proposed by Stuber (1991), cannot be ruled out.

The first species of *Fissurella* (*Fissurella*) probably arrived in Chile or Peru during the late Miocene or earliest Pliocene, since the subgenus was fully diversified by the late early Pliocene. In southern Peru, late Miocene antecedents to the modern Peruvian molluscan fauna were already established following a major species-level extinction event between 14 and 11 Ma (DeVries, 2001, 2002; DeVries & Frassinetti, 2003). Late Miocene rocky intertidal and mixed rock-and-sand subtidal molluscan faunas included numerous muricid genera and teguline trochids, as well as barnacles and the inarticulate brachiopod, *Discinisca* Dall, 1871 (DeVries, 1995, 1997, 2003, 2005a, 2005b). To this mix were added the turbinid, *Prisogaster* (about 10 Ma), the trochidine trochid, *Piscoacritia* DeVries and Hess, 2004 (about 7 Ma), and a thaid, *Purpura boliviana* Philippi, 1887 (about 7 Ma), all probably with western Pacific ancestry (DeVries and Hess, 2004; DeVries, 2006; DeVries, unpublished data). Fissurellids from the western Pacific Ocean or Indian Ocean could have arrived similarly. Other keyhole limpets (*Fissurellidea* group of genera) do show a disjunct South African and southern South American distribution (McLean, 1984b), which lends credence to a Southern Ocean origin for South American *Fissurella* (*Fissurella*).

The difficulty with a western Pacific or South African origin for South American *Fissurella* is that no obvious candidate for an ancestor exists. *Monodilepas monilifera* (Hutton, 1873), a New Zealand limpet with an early Miocene to Recent record (Dell,

1953; Beu & Maxwell, 1990), has a very broad foramen, cancellate sculpture, and lacks an aragonite/calcite shell structure. The same is true for some South African fissurellids [*Fissurellidea aperta* (Sowerby, 1825)]. Other South African fissurellids, including the coarsely ribbed modern *Fissurella mutabilis* Sowerby, 1834, and finely ribbed *F. natalensis* Krauss, 1848, as well as the smooth-shelled fossil *F. robusta* Sowerby, 1889, and *F. glarea* Carrington & Kensley, 1969 [late Miocene to late Pliocene (Roberts & Brink 2002; Franceschini & Compton 2004)], share some characters with South America *Fissurella*, but lack the aragonitic / calcitic shell layers.

CONCLUSIONS

Fissurella (*Fissurella*) are two-layered limpets (McLean, 1984a) from intertidal and shallow subtidal habitats along the coast of western and southern South America that may well constitute a monophyletic clade (Olivares, 2006). *Fissurella* appeared abruptly on the shores of western South America by the late early Pliocene, already fully diversified into coarsely ribbed, finely ribbed, and smooth-shelled groups that are largely congruent with molecularly defined clades (Olivares, 2006). The nearly nonexistent fossil record from northern Peru and examples of Neogene immigration by western Pacific taxa to the shores of western South America favor a Southern Ocean origin for *Fissurella* (*Fissurella*), although candidates for an ancestral fissurellid taxon are not obvious; late Miocene South African *F. robusta* and *F. glarea* might serve best as sister taxa.

Fissurella limpets are ecologically important members of rocky intertidal and subtidal communities in

Peru and Chile and are abundant enough to be the target of an artisanal harvest (Castilla & Fernandez, 1998). Their sudden appearance in the region during the late Miocene or early Pliocene is likely to have had an impact on trophic dynamics in communities where medium-sized and large limpets were mostly unknown [one exception: *Cellana fuenzalida* (Herm, 1969), a giant nacellid limpet from Chile and southern Peru (Herm, 1969; Lindberg and Hickman, 1986; DeVries, unpublished data)]. The interplay between recruitment of larval *Fissurella*, barnacles, and competition for space with a variety of algal species, for example, spelled out in the case of modern *F. picta* by Lopez et al. (1999), would have been repeated for an increasingly more diverse fissurellid fauna during the late early to late Pliocene, a time of global climate cooling (Ravelo et al., 2004) and mass extinction of marine mollusks in the Pliocene Peruvian Faunal Province (DeVries, 2001); opportunities for occupying new and abandoned niches may have expanded at that time.

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APPENDIX

List of Locality-Samples. 'GPS' signifies field measurement with GPS position.

Yauca	Panamerican Highway, roadcut descending towards village and river valley. Late Early Pliocene.	DV 1032	First curves at top of Huacllaco section. 15°52'59"S, 74°10'05"W (GPS; Chala 1:100,000 quadrangle). Includes samples DV 1032-1 (first curve in highway heading south, about 60–70 m in measured Huacllaco section, latest Pliocene) and DV 1032-2 (about 40–45 m in measured Huacllaco section, early late Pliocene). See Figure 2.
La Mina	Beach at La Mina, Paracas Peninsula. 13°54'32"S, 76°18'58"W (Pisco 1:100,000 quadrangle). Recent.	DV 1141-1	Northwest side Hueco La Zorra, beach. 14°02'46"S, 76°15'58"W (GPS; Punta Grande 1:100,000 quadrangle). Recent.
Lomas	Intertidal rocks, beach wrack, and trash near port village of Lomas. 15°34'S, 74°49'W (Yauca 1:100,000 quadrangle). Recent.	DV 1251-1	Quebrada Champeque, roadcut along Panamerican Highway. 15°48'42"S, 74°21'24"W (GPS; Chala 1:100,000 quadrangle). Late Pliocene.
DV 239-11	4.5 km south-southeast of Los Organos, along the Los Organos-Somatito road, cliffs near Occidental Petroleum wells 10531, 10529, and 10536. Lower 25 m of Taima Formation. Estimated coordinates 4°13'S, 81°06'30"W. Late Pliocene.	DV 1254	Roadcuts along Panamerican Highway 10 km southeast of Chala, above Playa Huacllaco. 15°53'S, 74°09'W (GPS; Chala 1:100,000 quadrangle). Samples from measured section (see Figure 2) and elsewhere include: DV 1254-2 (36.5 m), DV 1254-5 (44.2 m), DV 1254-6 (41.7 m), DV 1254-10 (48 m), DV 1254-14 (41 m), DV 1254-Bal5 (27 m), DV 1254-Bal10 (47.5 m), lowest cobbles (37 m). Late early Pliocene to late Pliocene. See Figure 2.
DV 401-1	Hueco La Zorra, beach. 14°02'31"S, 76°15'51"W (Punta Grande 1:100,000 quadrangle). Recent.	DV 1372-1	Punta Lomas, intertidal rocks and beaches. 15°34'S, 74°49'W (Yauca 1:100,000 quadrangle). Recent.
DV 465-1	Marine terrace north of Chala; elevation about 160–170 m above sea level. Middle Pleistocene.	DV 1418-1	South side Acari depression, upper beds. 15°34'50"S, 74°36'59"W (GPS; Yauca 1:100,000 quadrangle).
DV 599-2	Montemar, Pleistocene marine terraces. 15°32'05"S, 74°47'39"W (Yauca 1:100,000 quadrangle). Middle Pleistocene.	DV 1628-6	Huacllaco section southeast of Chala, sandstones of upper Unit III (see Figure 2). Chala 1:100,000 quadrangle. Late Pliocene.
DV 810-1	Quebrada Champeque, about 15 km north of Chala, marine terrace at 200 m above sea level. <i>Fissurella</i> specimens from surface of terrace; estimated to have been dropped by humans. Holocene.	DV 1635-2	Yauca Depression, western side Panamerican Highway. 15°39'33"S, 75°34'54"W (GPS; Yauca 1:100,000 quadrangle). Late early Pliocene.
DV 923	Knolls on southeast side of Río Acari. 15°36'29"S, 74°37'53"W (GPS; Yauca 1:100,000 quadrangle). Early to late Pliocene. (See Figure 3.) Samples from measured section include DV 923-1 and DV 923-1e (both about 9 m) and DV 923-1a (0.2 m).	LACM 75-31	Intertidal zone and beach, Isleta Concón, north of Viña del Mar, Chile. 32°52'S, 71°33'W. Recent. Collected by J. H. McLean, 1975.
		LACM 75-32	Intertidal zone, Punta El Lacho, north of Cartagena, Chile. 33°30'S, 71°39'W. Recent. Collected by J. H. McLean, 1975.

Revision of the Protobranch Species Described by Dautzenberg & Fischer (1897) with Description of a New Species and Taxonomic Comments on *Bathyspinula* (Bivalvia, Nuculanoidea)

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Abstract. In 1897, Philippe Dautzenberg and Henry Fischer described six deep water protobranchs from the North Atlantic (*Princesse-Alice* expeditions, 1894, 1896): *Leda excisa* (Philippi) var. *subexcisa*, *Leda bernardi*, *Leda allaudi*, *Leda mirmidina*, *Leda mabiliei* and *Malletia perrieri*. Almost all of these taxa are only known from the original description, with no further records in the modern literature. The present revision, based on the original material, led to the following combinations: *Bathyspinula subexcisa*, *Ledella bernardi*, *Yoldiella allaudi* (lectotype designated), *Microgloma mirmidina*, *Nuculana mabiliei* and *Tindaria perrieri*. A new species is described as *Yoldiella dautzenbergi* from material misidentified as *Leda allaudi*. Taxonomic comments are given for the genus *Bathyspinula* Filatova, 1958. The subfamily Bathyspinulinae Coan & Scott, 1997 (= Spinulinae Allen & Sanders, 1982 *nom. inval.*), formerly in the family Nuculanidae, is raised to full family rank within the Nuculanoidea. *Tindariopsis* Verrill & Bush, 1897 is also assigned to the Bathyspinulidae.

INTRODUCTION

Dautzenberg & Fischer (1897) described six new deep water protobranchs from the North Atlantic (*Princesse-Alice* expeditions 1894, 1896): *Leda excisa* (Philippi) var. *subexcisa*, *Leda bernardi*, *Leda mabiliei*, *Leda allaudi*, *Leda mirmidina* and *Malletia perrieri*. Almost all of these taxa are only known from the original description, with no further records in the modern literature on the North Atlantic molluscs. A single species, *Spinula subexcisa* (Dautzenberg & Fischer, 1897), was included in two taxonomic works (Clarke, 1961; Allen & Sanders, 1982), but without examination of the type material. The present work offers a systematic revision of these poorly known species, based on the original material. This paper also gives an occasion to discuss the taxonomy of the genus *Bathyspinula* and its systematic position within the Nuculanoidea.

MATERIAL AND METHODS

The *Princesse-Alice* stations from which Dautzenberg & Fischer (1897) described the species dealt with in the present work are reported in Figure 1. Dautzenberg (1927) renumbered all the stations from the *Princesse-Alice*, *Hirondelle* and *Prince de Monaco* expeditions (1886–1913) as a single series, with longitudes west of Greenwich, whereas the original longitudes were west of Paris. In the present work, station numbers and longitudes are according to Dautzenberg's (1927) list,

with the original station number in parenthesis. Dautzenberg (1927) also reported the same descriptions and illustrations as those originally published by Dautzenberg & Fischer (1897).

The type material is from the Musée Oceanographique de Monaco, the Institut Royal des Sciences Naturelles de Belgique, Bruxelles and the Monterosato collection, Museo Civico di Zoologia, Rome. A list of this material is reported in Table 1.

The nuculanid classification adopted in the present work follows the scheme by Ockelmann & Warén (1998), except for the position of the genus *Bathyspinula*.

The following abbreviations are used: exp(s) – expedition(s), sh(s) – complete shell(s), paired valves; v(s) – valve(s); IRScN – Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MOM – Musée Oceanographique de Monaco, MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MZR – Museo Civico di Zoologia, Rome.

SYSTEMATICS

Family Nuculanidae H. & A. Adams, 1858

Genus *Nuculana* Link, 1807

Nuculana mabiliei (Dautzenberg & Fischer, 1897)

(Figures 2a–e)

Leda mabiliei Dautzenberg & Fischer, 1897:207, pl. 6, figs 9, 10.

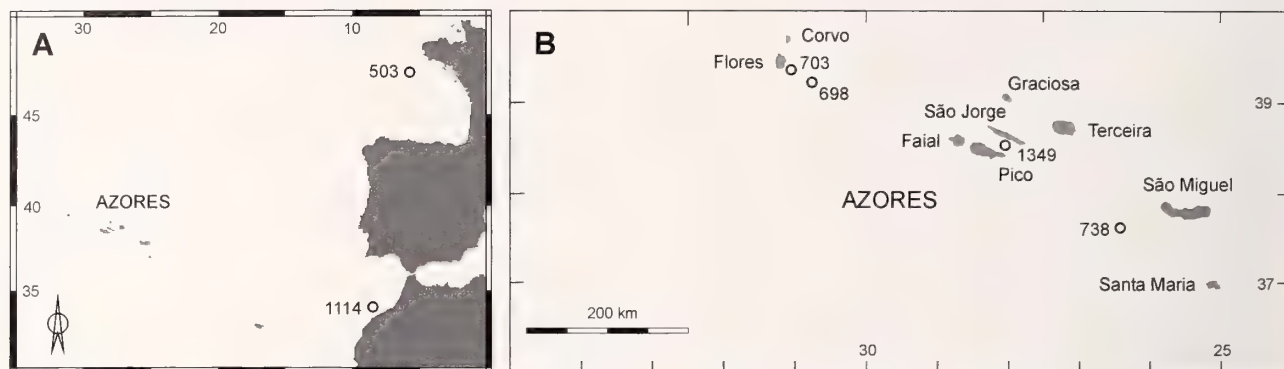


Figure 1. Monaco expeditions, stations 503, 698, 703, 738, 1114, 1349.

Leda mabiliei – Dautzenberg, 1927:291, pl. 8, figs 25, 26.

Types: Monaco exps., st. 503 (*Princesse-Alice* 1894, st. 101), 47°10'N, 5°47'45"W, 748–1262 m, 1 v, MOM 21160, holotype.

Distribution: Only known from a single deep water station off the Bay of Biscay.

Remarks: The single, poorly preserved type right valve is notably robust and convex, triangular-elongate in shape, with a short, truncate, bicarinate rostrum and a wide, slightly concave postero-dorsal area. The sculpture consists of commarginal ridges, somewhat irregular in spacing and strength, slightly coarser posteriorly (Figures 2a, d). The hinge is relatively strong, with a triangular, oblique ligament pit (Figure 2e). A shallow, poorly defined rostral ridge is present internally. The rostrum tip is slightly broken (Figure 2d), giving appearance of an oblique truncation, as in the original description (*rostrum oblique truncatum*).

Leda mabiliei can be easily assigned to the genus *Nuculana*. It is different in many respects from the two well known North Atlantic species of *Nuculana*, i. e. *N. pernula* (O.F. Müller, 1776) and *N. minuta* (O.F. Müller, 1776). Good illustrations of these two species were reported by Schiøtte & Warén (1992). Due to the short rostrum, *Nuculana mabiliei* is more similar to *N.*

minuta, from which it differs mainly by being less elongate and more triangular in shape, more robust and convex.

The occurrence of *N. mabiliei* in a deep water station is puzzling, as species of this genus typically occur in shallow waters. Moreover, this species is notably different from some deep water nuculanids with a long, slender and bent rostrum which can be assigned to *Thestyleda* Iredale, 1929 (Di Geronimo & La Perna, 1997). The valve of *N. mabiliei* could have undergone a down-slope transport from outer shelf bottoms, as also suggested by its poor preservation status.

Genus *Ledella* Verrill & Bush, 1897

Ledella bernardi (Dautzenberg & Fischer, 1897)

(Figures 3a–f)

Leda bernardi Dautzenberg & Fischer, 1897:206, pl. 6, figs 5, 6.

Leda bernardi – Dautzenberg, 1927:289, pl. 8, figs 21, 22.

Nuculana bernardi – Clarke, 1962:52.

Types: Monaco exps., st. 738 (*Princesse-Alice* 1896, st. 109), 37°40'N, 26°25'15"W, 1919 m, 1 v, MOM 21158, holotype. Same station as holotype, 2 vs, IRScN 1238/5.

Distribution: Only known from a single deep water station, west of São Miguel, Azores.

Remarks: *Leda bernardi* was described from a single right valve (MOM) (Figures 3a–c), but two other valves from the same station as the holotype are present at IRScN (Figures 3d–f): one of them is fairly well preserved and younger, the other is badly preserved.

The shell is ovate-elongate, not particularly convex, moderately robust, shortly rostrate, with a very shallow subrostral sinuation and an obscure posterior keel. The umbo is strongly opisthogyrate. The surface bears growth striae and ill defined, widely spaced commar-

Table 1
List of the type material.

	MOM	IRScN	MZR
<i>Leda excisa</i> var. <i>subexcisa</i>		5 vs	2 vs
<i>Leda bernardi</i>	1 v	2 vs	
<i>Leda mabiliei</i>	1 v		
<i>Leda allaudi</i>	1 v	1 v	
<i>Leda mirmidina</i>	2 vs	16 vs	
<i>Malletia perrieri</i>	1 v		

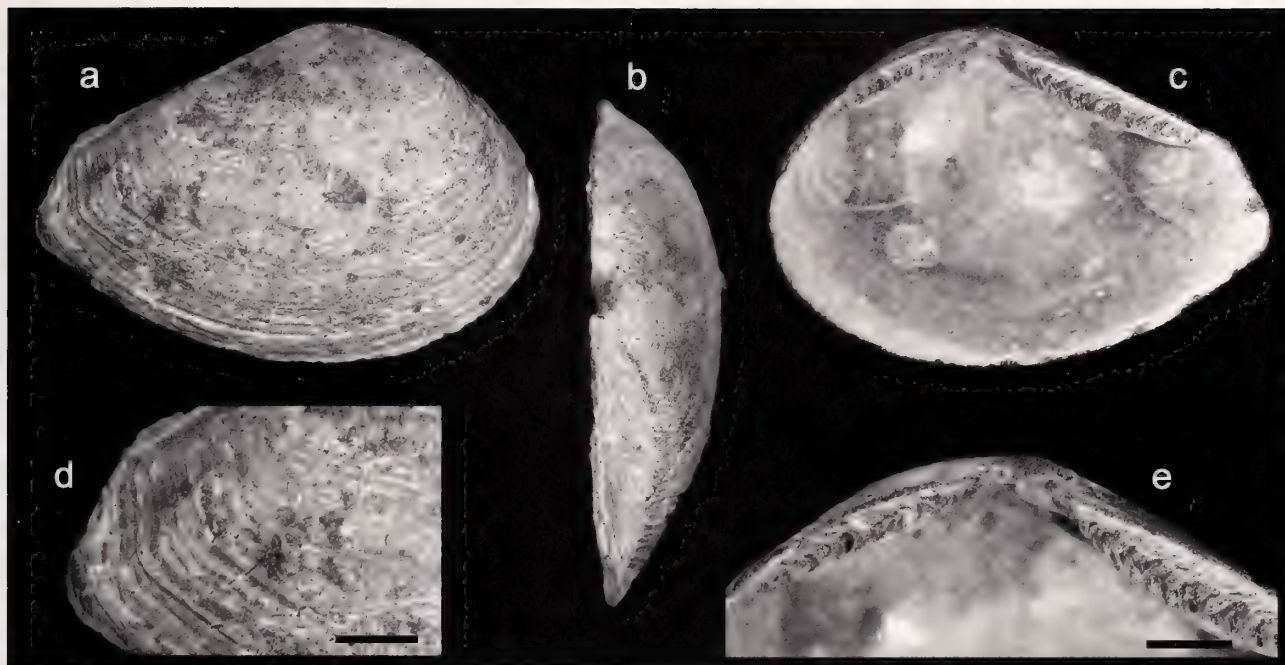


Figure 2. *Nuculana mabiliei* (Dautzenberg & Fischer, 1897). a–e. Holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 9, 10), length 10.35 mm, MOM 21160.

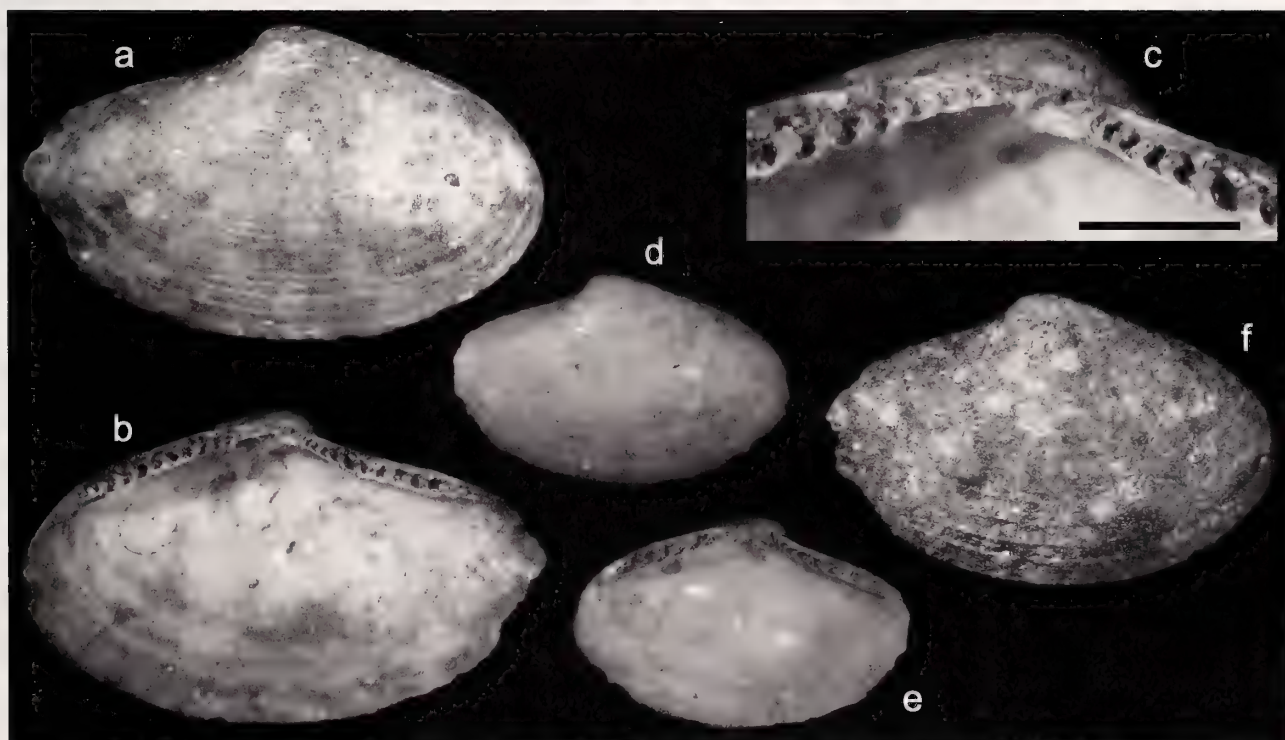


Figure 3. *Ledella bernardi* (Dautzenberg & Fischer, 1897). a–c. Holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 5, 6), length 9.40 mm, scale bar = 1 mm, MOM 21158. d, e. topotype, length 6.11 mm, IRScN 1238. f. topotype, length 8.20 mm, IRScN 1238/5.

ginal ridges, becoming better defined near the ventral margin. The hinge is relatively strong, with a triangular, oblique ligament pit. The pallial sinus is well defined, not particularly deep. The larval shell is worn in all three valves.

This species shows remarkable similarities with a group of deep-water North Atlantic species which includes *Leda oxira* Dall, 1927, *Leda semen* Smith, 1885, *Ledella parva* Verrill & Bush, 1898 and *Ledella similis* Allen & Hannah, 1989. They share an ovate-elongate shell, a short rostrum, a poorly defined subrostral sinuation and a strongly opisthogyrate umbo. Of these, *Ledella similis* is the only species known from the West European Basin (Allen & Hannah, 1989), whereas *Leda oxira*, *L. semen* and *Ledella parva* are from the Western Atlantic (Smith, 1885; Verrill & Bush, 1898; Dall, 1927; Allen & Hannah, 1989). All of them were referred to *Ledella* by Allen & Hannah (1989) who also attempted to synonymise *Ledella parva* with *Leda semen* (see also Verrill & Bush, 1898). This problem is hard to resolve, since the type material of *Leda semen* is destroyed (Allen & Hannah, 1989), but the examination of the original illustrations (Smith, 1885:pl. 19, figs 2, 2a; Verrill & Bush, 1898:pl. 81, fig. 1) suggests a distinct status for both species. Another deep water species, *Ledella librata* Dell, 1952 from the Challenger Plateau, New Zealand, seems notably similar to the group of Atlantic species.

The systematic position of these species is not clear. They actually recall *Ledella*, but differ by being notably elongate and with a strongly opisthogyrate umbo. The species of *Ledella* usually have a rather sharp posterior keel, a well defined subrostral sinuation and a pointed rostrum (e.g., Warén, 1978; Allen & Hannah, 1989; La Perna et al., 2004). However, no other genus so far described seems to provide a better position for this group of species.

Genus *Yoldiella* Verrill & Bush, 1897

Yoldiella allaudi (Dautzenberg & Fischer, 1897)

(Figures 4a–d)

Leda allaudi Dautzenberg & Fischer, 1897:207, pl. 6, figs 7, 8.

Leda allaudi – Dautzenberg, 1927:290, pl. 8, figs 23, 24.
Nuculana allaudi – Clarke, 1962:52.

Types: Monaco exps., st. 703 (*Princesse-Alice* 1896, st. 74), 39°21'20"N, 31°06'W, 1360 m, 1 v, MOM 21156, lectotype; 1 v, IRScN, 1238/03, paralectotype.

Distribution: Only known from a single, deep water station, east of Flores, Azores. Other records (Daut-

zenberg & Fischer, 1897; Dautzenberg, 1927) cannot be confirmed.

Remarks: The shell of *Yoldiella allaudi* is delicate, markedly convex, ovate, distinctly inequilateral in shape and with a sculpture of thin, irregularly spaced commarginal ridges. The hinge is thin, with anterior and posterior rows of teeth of similar length, separated by a small, triangular ligament pit. The larval shell is ovate, 170 µm in maximum length.

The material of *Leda allaudi* at MOM consists of a single valve (st. 703), illustrated by Dautzenberg & Fischer (1897:pl. 6, figs 7, 8). Three valves from the same station are present at IRScN: one of them is *Leda allaudi*, whereas the two other valves belong to a new species herein described.

Additional material labelled as *Leda allaudi*, from two other stations, is present at IRScN: Monaco exps., st. 1349, 38°35'30"N, 28°05'45"W, 1250 m, Azores and st. 1114, 33°59'30"N, 8°12'45"W, 851 m, off Casablanca (Figure 1), but no specimen proves to be *Leda allaudi*. The material from the Azores includes 3 valves of an unidentified species, here kept as *Yoldiella* sp. A, and two poorly preserved, unidentifiable shells. The material from off Casablanca includes *Yoldiella semistriata* (Jeffreys, 1879) (2 vs, 1 sh), *Yoldiella seguenzae* Bonfitto & Sabelli, 1995 (2 vs) and an unidentified species (1 v), here kept as *Yoldiella* sp. B. Some of this material is illustrated in Figure 5.

In order to fix the identity of *Leda mabiliei*, a lectotype was designated (Figures 4a, b): it is the left valve from st. 703 (MOM), illustrated by Dautzenberg & Fischer (1897). The other valve from the same station at IRScN is a paralectotype (Figures 4c, d).

None of the many species of *Yoldiella* known from the Atlantic (e.g., Warén, 1989; Allen et al., 1995; Salas, 1996) seems particularly similar to *Y. allaudi*, except for *Y. subaequilatera* (Jeffreys, 1879) and the following new species, as discussed below.

Yoldiella dautzenbergi n. sp.

(Figures 4e–h)

Type material: Holotype and one paratype (left valves), IRScN, 1238/03.

Type locality: Monaco exps., st. 703 (*Princesse-Alice* 1896, st. 74), 39°21'20"N, 31°06'W, 1360 m.

Etymology: Named after Philippe Dautzenberg, Belgian malacologist (1849–1935).

Description: Shell small, thin walled, ovate, poorly elongate, subequilateral, moderately convex. Umbo at mid line, small, slightly opisthogyrate, distinctly protruding from shell outline. Posterior end well rounded, anterior end obscurely rostrate, slightly

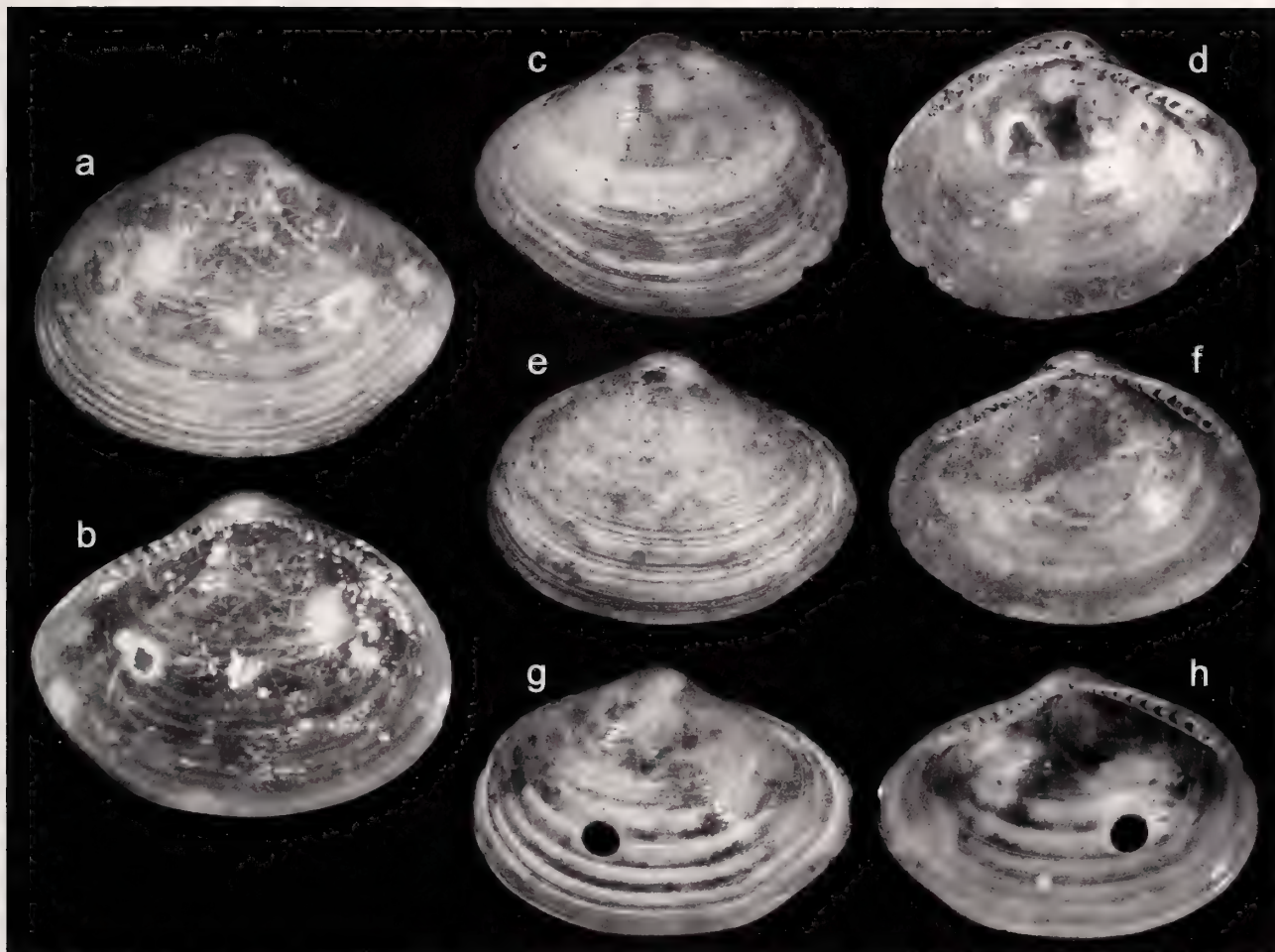


Figure 4. a–d. *Yoldiella allaudi* (Dautzenberg & Fischer, 1897). a, b Lectotype (Dautzenberg & Fischer, 1897:pl. 6, figs 7, 8), length 5.16, MOM 21156. c, d. Paralectotype, length 4.01 mm, IRSn 1238/03. e–h *Yoldiella dautzenbergi* n. sp. e, f. Holotype, length 4.02 mm, IRSn 1238/03. g, h. Paratype, length 4.08 mm, IRSn 1238/03.

narrower than anterior. Ventral margin moderately convex, with a faint slope break at postero-ventral transition. Subrostral sinuation almost absent. Sculpture consisting of growth striae and well incised, irregularly spaced commarginal lines, giving appearance of wide, flat ribs. Hinge plate thin, delicate. Dentition taxodont, with chevron-shaped teeth in two series of similar length, with about ten teeth anteriorly and posteriorly. Anterior row slightly convex, posterior row almost straight. Ligament pit small, triangular, sunken. Adductor muscle scars ovate, of similar size. Pallial sinus narrow, moderately deep. Prodissoconch ovate, 280 μ m in maximum diameter.

Measurements: holotype 4.02 mm in length, 2.97 mm in height, 1.05 mm in width; paratype 4.08 \times 2.90 \times 0.95 mm.

Distribution: Only known from a single, deep water station, east-of Flores, Azores.

Remarks: The material of *Yoldiella dautzenbergi* n. sp. is from the lot of *Leda allaudi* at IRSn (see under *Yoldiella allaudi*).

Yoldiella dautzenbergi is much less convex, slightly less elongate and more equilateral than *Y. allaudi*, with the posterior end just slightly narrower than the anterior one. The umbo is less opisthogyrate and slightly smaller, the ventral margin less convex. In both species there is a faint slope break at the postero-ventral transition, but it is more distinct in *Y. dautzenbergi*. The subrostral sinuation is almost absent in *Y. dautzenbergi* and the sculpture consists of deeply incised, irregularly spaced commarginal lines, rather than of thin ridges. The larval shell is smaller than in *Y. allaudi*. The largest valve of *Y. allaudi* is about 5 mm in length, whereas the two valves of *Y. dautzenbergi* are about 4 mm, but the material is too scant for assessing a size difference between the two species.

A close resemblance also exists with *Yoldiella*

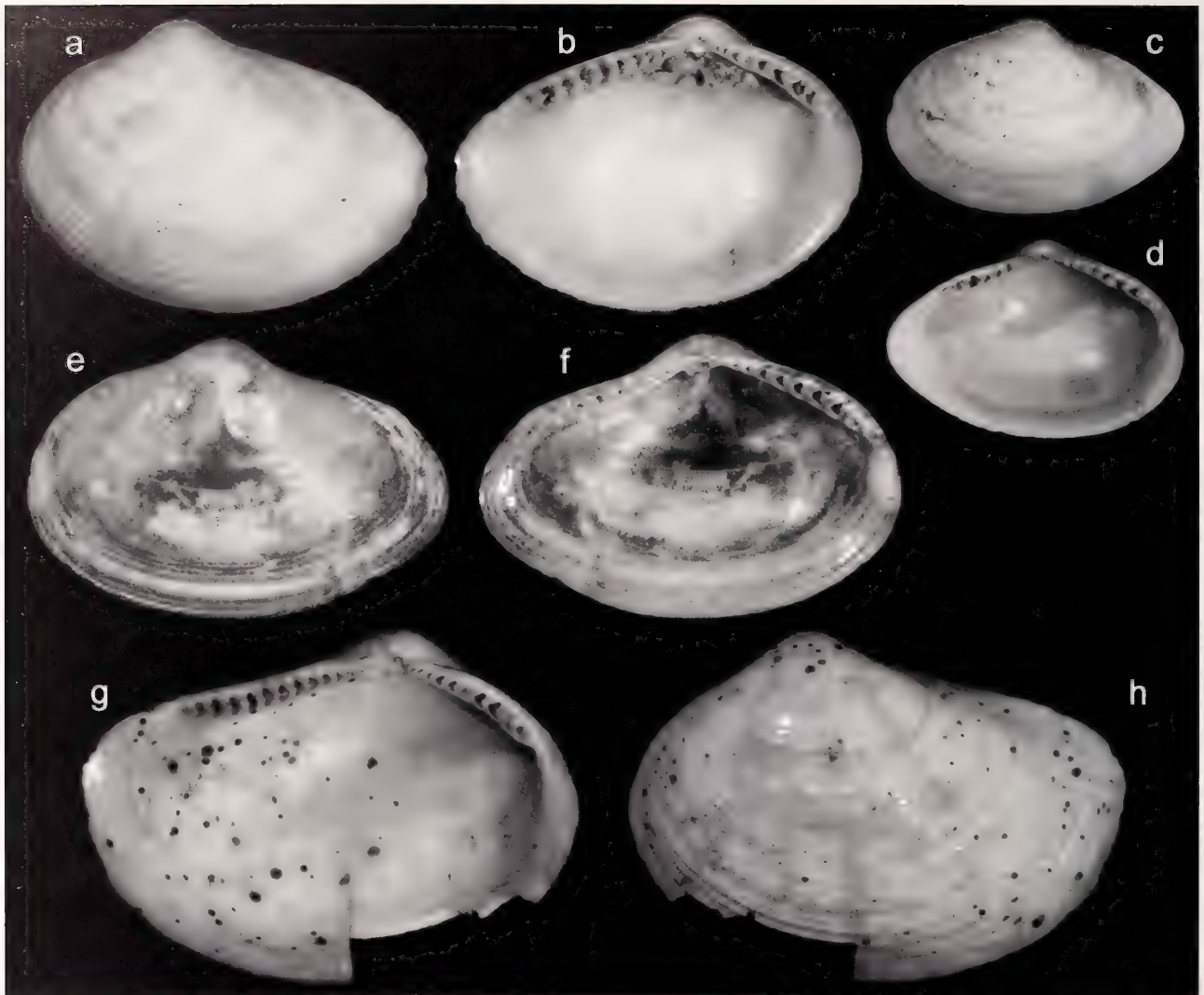


Figure 5. a, b. *Yoldiella semistriata* (Jeffreys, 1879). Monaco expeditions (1901), st. 1114, off Casablanca, length 3.56 mm, IRScN 1238/03. c, d. *Yoldiella seguenzae* Bonfitto & Sabelli, 1995. Monaco expeditions (1901), st. 1114, off Casablanca, length 2.58 mm, IRScN 1238/03. e, f. *Yoldiella* sp. A, Monaco expeditions (1902), st. 1349, Azores, length 3.62 mm, IRScN 1238/03. g, h. *Yoldiella* sp. B. Monaco expeditions (1901), st. 1114, off Casablanca, length 4.86 mm, IRScN 1238/03.

subaequilatera (Jeffreys, 1879), a poorly known deep water species from the Northeast Atlantic, dealt with by Warén (1989:p. 235, figs 10a, b). The new species is slightly less elongate and less equilateral than *Y. subaequilatera*, and more convex, with a narrower umbonal angle and with a better defined sculpture.

Genus *Microgloma* Sanders & Allen, 1973

Microgloma mirmidina (Dautzenberg & Fischer, 1897)

(Figures 6a–g)

Leda mirmidina Dautzenberg & Fischer, 1897:208, pl. 6, figs 1–5.

Leda mirmidina – Dautzenberg, 1927:292, pl. 8, figs 27–30.

Nuculana mirmidina – Clarke, 1962:53.

Types: Monaco exps., st. 698 (*Princesse-Alice* exp. 1986, st. 69), 1846 m, 39°11'N, 30°44'40"W, 2 vs, MOM 21157, syntypes; 16 vs, MIRSCh 1239/02, syntypes.

Distribution: Only known from a single, deep water station, south-east of Flores, Azores.

Remarks: The position of the family Pristiglomidae Sanders & Allen, 1973 in the superfamily Nuculoidea, as proposed by Sanders & Allen (1973), was criticized by Ockelmann & Warén (1988) who assigned *Pristi-*

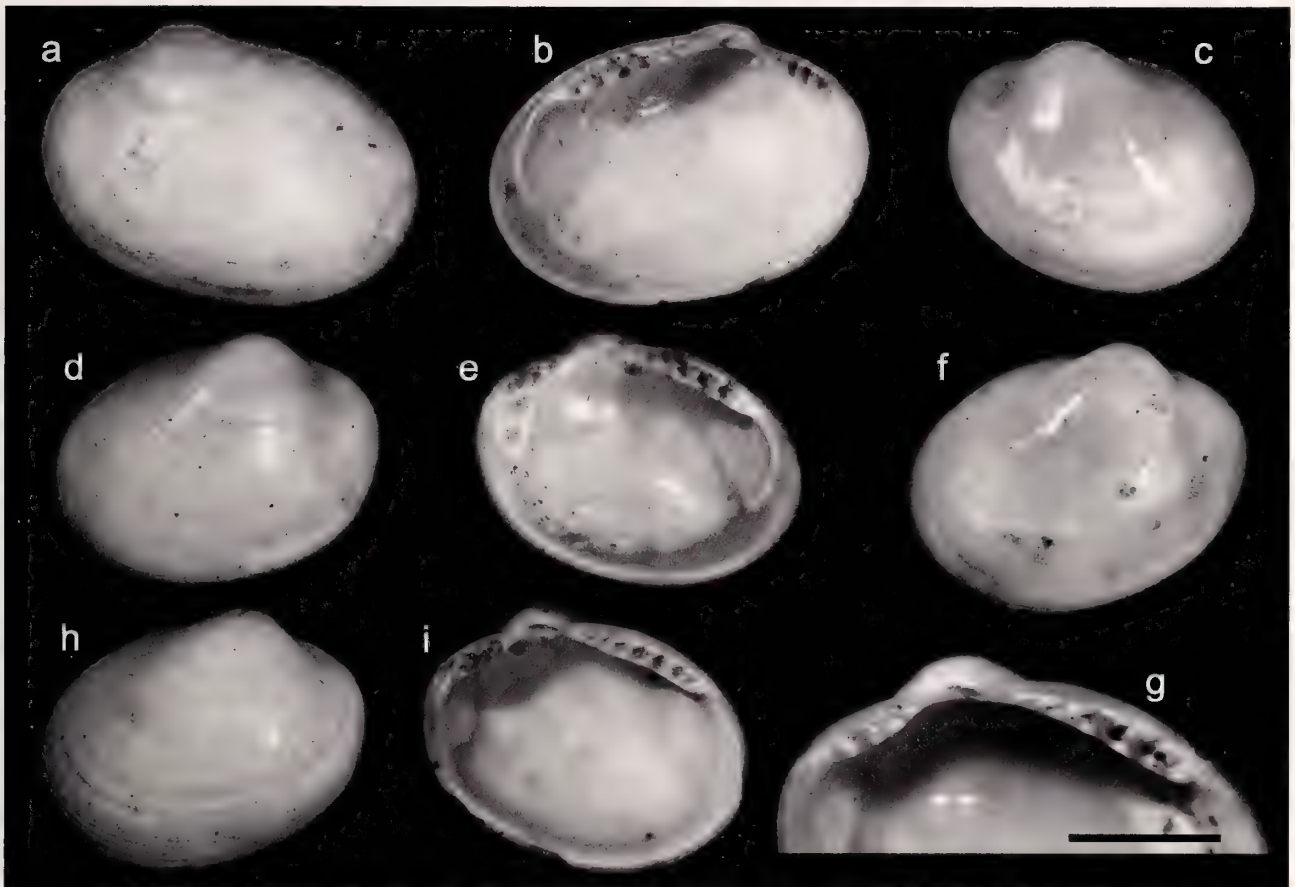


Figure 6. a–g. *Microgloma mirmidina* (Dautzenberg & Fischer, 1897). a, b. Syntype (Dautzenberg & Fischer, 1897:pl. 6, figs 12, 14), length 1.84 mm, IRScN 1239/02 (ligament pit enlarged by breaking or corrosion). c. Syntype, length 1.47 mm, IRScN 1239/02. d, e. Syntype, length 1.58 mm, IRScN 1239/02. f, g. Syntype, length 1.63 mm, scale bar = 0.5 mm, IRScN 1239/02. h, i. Syntype, length 1.57 mm, MOM 21157.

gloma Dall, 1900 and *Microgloma* Sanders & Allen, 1973 to the Nuculanidae. They also presented strong evidence for the progenetic character of *Microgloma*.

Three further species of *Microgloma* were known, all from the Atlantic (Sanders & Allen, 1973; Ockelmann & Warén, 1998): *M. yongei* Sanders & Allen, 1973 (type species), *M. tumidula* (Monterosato, 1880) (= *M. turnerae* Sanders & Allen, 1973) and *M. pusilla* (Jeffreys, 1879). The last two species occur in European waters. Another European species, *Phaseolus guilonardi* Hoeksema, 1983 is provisionally placed in *Microgloma*, but it clearly belongs to a different group, as discussed by Ockelmann & Warén (1998) and La Perna (2003).

Microgloma mirmidina is somewhat similar to *M. yongei* and *M. tumidula* in the ovate-subrectangular shape, whereas *M. pusilla* is distinctly egg-shaped. All these species have a comparatively robust, notably convex shell, with a sculpture of thin ridges near the ventral margin. The muscle scars are slightly buttressed

in *M. mirmidina* and generally well-defined in the other species.

The largest syntype is 1.84 mm in shell length (Figures 6a, b), the others 1.5–1.6 mm. *Microgloma mirmidina* therefore is notably larger than *M. yongei*, *M. tumidula* and *M. pusilla* which are about 1 mm in shell length (Allen & Sanders, 1973; Ockelmann & Warén, 1998). The shell shape changes notably with growth, from dorso-posteroventrally oblique to posteriorly elongate, whereas the other species grow almost isometrically and equilaterally, as seen in the growth series of *M. yongei* and *M. tumidula* reported by Sanders & Allen (1973). This is probably due to the relatively large size of *M. mirmidina*, allowing this species to follow a growth pattern more similar to that of normal sized bivalves, whereas the other species are too small for manifesting marked allometric changes. At a size larger than 1.3–1.5 mm, the growth of *M. mirmidina* produces a stepped shell edge, giving a box-

like appearance. As observed by Ockelmann & Warén (1998), such a growth pattern which at a smaller extent occurs in the other species of *Microgloma*, provides an increase in shell volume and counterbalances the effects of miniaturization.

Besides the small size, Ockelmann & Warén (1998) remarked two other synapomorphies for the *Microgloma* species: the enlarged innermost teeth of the left valve and the radially wrinkled surface of the prodissococonch. The first character is not present in *M. mirmidina* (Figure 6g), but admittedly it is not always present or clearly developed in the other species (e.g., Ockelmann & Warén, 1998:fig. 9f). However, the hinge of *M. mirmidina* is similar to that of the congeners, with slightly chevron-shaped to rather stout teeth and a small, elongate ligament pit. The ligament pit is slightly oblique, with the anterior end apparently external or semi-external (Figure 6g). It is similar to the oblique ligament pit of a juvenile specimen of *Yoldiella philippiana* (Nyst, 1845) illustrated by Ockelmann & Warén (1998:fig. 3b), which differs by being posteriorly external. This supports the hypothesis by Ockelmann & Warén (1998:11) for the progenetic origin of *Microgloma* from *Yoldiella* or *Ledella*.

The larval shell of *M. mirmidina* is ovate, about 180 µm in length, notably smaller than that of *M. yongei* (290 µm) and *M. tumidula* (260–270 µm), more similar to that of *M. pusilla* (195–218 µm), according to the data by Sanders & Allen (1973) and Ockelmann & Warén (1998). Under optical magnification the prodissococonch surface shows an unresolved sculpture and it was not possible to ascertain if it corresponds to the radially wrinkled pattern reported by Ockelmann & Warén (1998).

Family Bathyspinulidae Coan & Scott, 1997

Genus *Bathyspinula* Filatova, 1958

Filatova & Shileyko (1984) pointed out the preoccupied status of *Spinula* Dall, 1908 by *Spinula* Herrich-Schaeffer, 1856 (Lepidoptera). They replaced the genus name *Spinula* with *Bathyspinula* Filatova, 1958, formerly subgenus of *Spinula*, and erected the new subgenus *Acutispinula*. Accordingly, *Bathyspinula* includes the subgenera *Bathyspinula* (*Bathyspinula*) and *B. (Acutispinula)*. Species of the latter differ by a finer, almost absent sculpture and a longer, sharper rostrum (Allen & Sanders, 1982; Filatova & Shileyko, 1984; Coan et al., 2000). The type species are *Bathyspinula (B.) oceanica* (Filatova, 1958) and *Bathyspinula (Acutispinula) calcar* (Dall, 1908), respectively.

Allen & Sanders (1982) erected the monogeneric subfamily Spinulinae (invalidly based on an junior homonym, replaced with Bathyspinulinae by Coan & Scott, 1997) in the family Nuculanidae to contain the genus *Bathyspinula*, whereas Filatova & Shileyko

(1984) included this genus in the subfamily Ledellinae, family Ledellidae Allen & Sanders, 1982. Ockelmann & Warén (1998) kept the Nuculanidae as a single, undivided family; a systematic view markedly different from the multi-taxa classification by Allen & Sanders (1986). However, as discussed below, there are good reasons for keeping *Bathyspinula* in a separate position, at a full family rank.

The adults of *Bathyspinula* possess a long, mainly external, amphidetic ligament, with a small internal component (Allen & Sanders, 1982; Di Geronimo & La Perna, 1996) (Figures 7a, b; see also the good illustrations by Knudsen, 1970). The internal ligament tends to a semi-external position and part of it can be seen externally, between the umbones of closed valves (Figure 7b). This condition is more evident in the juvenile stages, which possess a proportionally larger, clearly semi-external ligament pit (Figure 7c). The other nuculanids, such as *Nuculana*, *Ledella* and *Yoldiella* have a juvenile, external amphidetic ligament becoming fully internal with growth, as well-documented by Ockelmann & Warén (1998), or leaving a small external relict as in *Jupiteria* (La Perna et al., 2004). The ligament of *Bathyspinula* is then much more similar to that of the families Malletiidae H. & A. Adams, 1858 (Sanders & Allen, 1985), Tindariidae Verrill & Bush, 1897 (Sanders & Allen, 1977) and Neilonellidae Shileyko, 1989 (Warén, 1989; Allen & Sanders, 1996; La Perna, 2007), all with a well-developed external ligament and a smaller internal component in the adults, than to that of the other nuculanids. None of these families provide a suitable position for *Bathyspinula*, for the following reasons: 1) malletiids have a subrectangular, posteriorly truncate or bluntly rostrate, poorly sculptured shell; 2) neilonellids have an ovate, poorly rostrate shell with no trace of subrostral sulcus and postero-ventral sinuation; 3) tindariids have a roundish, not rostrate shell and are asiphonate (*Bathyspinula* has well developed, united siphons: Filatova & Shileyko, 1984; Allen & Sanders, 1982). A full family rank is therefore adopted for the Bathyspinulinae Coan & Scott, 1997 (= Spinulinae Allen & Sanders, 1982).

The family Bathyspinulidae also provides a suitable position for *Tindariopsis* Verrill & Bush, 1897, instead of the Tindariidae (Verrill & Bush, 1898), Malletiidae (Dall, 1898; Vokes, 1980; Laghi, 1986) or even Nuculanidae, subfamily Ledellinae (Allen & Sanders, 1996). The type species, *Malletia (Tindaria) agathida* Dall, 1889 has the same ligament type as *Bathyspinula*, with a "well-marked dorsal ligamental furrow and a small notch or «socket» under the beak" (Verrill & Bush, 1897, 1898; see also Dall, 1898:582). *Tindariopsis agathida* has a shallow pallial sinus (Dall, 1898; Allen & Sanders, 1996) and cannot be assigned to the Tindariidae (which lack a pallial sinus), as suspected by Verrill & Bush (1898). On the other hand, the pointed, keeled

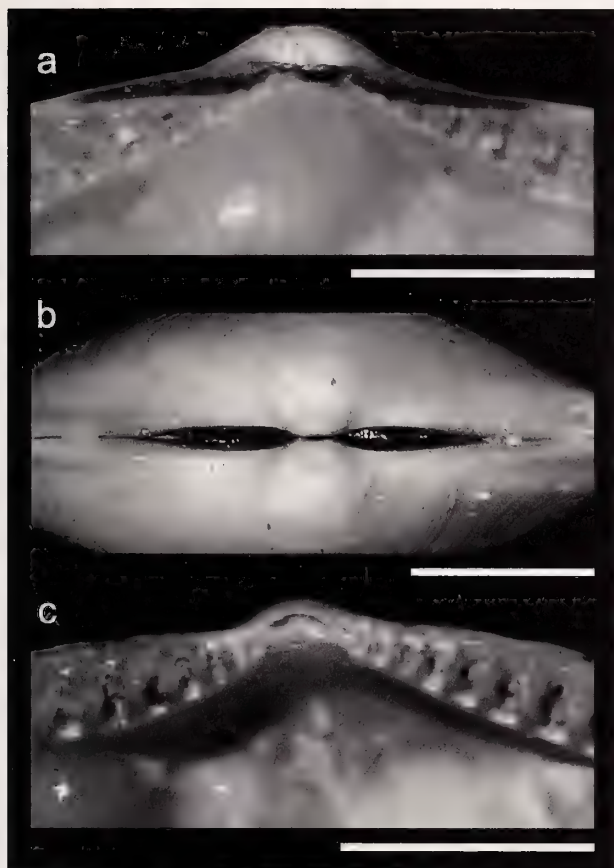


Figure 7. a–c. Ligament characters of *Bathyspinula*. a. *Bathyspinula subexcisa* (Dautzenberg & Fischer, 1897), Challenger exp. (1973), st. 4, length 5.01 mm, MCZ 348787. b. *Bathyspinula hilleri* (Allen & Sanders, 1982), st. DS23, length 4.93 mm, MCZ 348807. c. *Bathyspinula excisa* (Philippi, 1844), Archi, southern Calabria, Early-Middle Pleistocene, length 3.25 mm, author's coll. Scale bars: = 1 mm.

rostrum and the well-defined subrostral sulcus make *Tindariopsis* similar to *Bathyspinula* and markedly different from malletiids and neilonellids, whereas the resemblance with *Ledella* is due to convergence. A series of good illustrations, though with some misidentification, was published by Laghi (1986:pl. 8, figs 1a–6c; *Nuculana* cfr. *pusio* Philippi of figs 1a,b is a *Tindariopsis* species), including the holotype of *Tindariopsis agathida*.

Bathyspinula (*B.*) *subexcisa* (Dautzenberg & Fischer, 1897)

(Figures 7a, 8a–k, r, s)

Leda excisa var. *subexcisa* Dautzenbeg & Fischer, 1897: 205.

Leda (*Neilo*) *excisa* var. *subexcisa* – Dautzenberg, 1927:295.

Spinula subexcisa – Clarke, 1962:52 (?).

Spinula subexcisa – Allen & Sanders, 1982:21, figs 22, 23, 27, 28.

Types: Monaco exps., st. 698 (*Princesse-Alice* 1896, st. 69), 39°11'N, 30°44'40"W, 1846 m, Azores, 5 vs, IRScN 1238/01, syntypes; Monterosato coll., 2 vs, MZR 14423, syntypes.

Other material examined: Challenger exp. (1973), st. 4, 56°52'N, 10°01'W, 1993 m, Rockall Trough, 4 shs, 1 v, MCZ 348787 (Allen & Sanders, 1982). Chain 106 exp. (1972), st. 318, 50°26.8'–50°27.3'N, 13°19.9'–13°20.9'W, 2506 m, off West Ireland, 5 shs, MCZ 348785.

Distribution: *Bathyspinula subexcisa* is known from the North Atlantic (West Europe and Azores), in 1846–2506 m.

Remarks: The history of *Bathyspinula subexcisa* is closely linked to *Nucula excisa* Philippi, 1844, described from the Plio-Pleistocene of Southern Italy (Philippi, 1844: p. 46, pl. 15, fig. 4; Di Geronimo & La Perna, 1996). According to Allen & Sanders (1982), the records of *Malletia excisa* by Jeffreys (1876, 1879) and of *Leda excisa* by Smith (1885) from the North Atlantic could have been based either on *Bathyspinula subexcisa* or on *Bathyspinula hilleri* Allen & Sanders, 1982, both occurring in the North Atlantic, the latter with a much wider Atlantic distribution. Also the record of *Spinula subexcisa* from the South Atlantic by Clarke (1961) was probably based on a different species, possibly *Bathyspinula hilleri*. He compared his specimens with material from the Jeffreys coll. and found them “identical to *M. excisa*, as Jeffreys understood it.”

This is the first time the type material of *Bathyspinula subexcisa* is revised. The sole illustrations so far available for this species were the drawings by Allen & Sanders (1982).

The most obvious differences from *Bathyspinula excisa* (Figures 8n–q) lie in the shallower subrostral sinus and in the finer sculpture. *Bathyspinula subexcisa* also differs by being less convex and more delicate, with a shorter rostrum and a less distinct rostral keel.

Allen & Sanders (1982) reported *Bathyspinula subexcisa* from a single station (Challenger exp. 1973, st. 4). Some of this material was examined (Figures 8f–i) and it actually matches the type material. Microscopic, anastomosing radiating lines, are present along the subrostral sulcus; they are similar to the microsculpture present in *Bathyspinula excisa* (Di Geronimo & La Perna, 1996:pl. 2, figs 1, 1a). This character is not visible in the type material of *B. subexcisa*, most probably due to the poor preservation. Other specimens (Chain 106 exp. 1972, st. 318) differ by having a

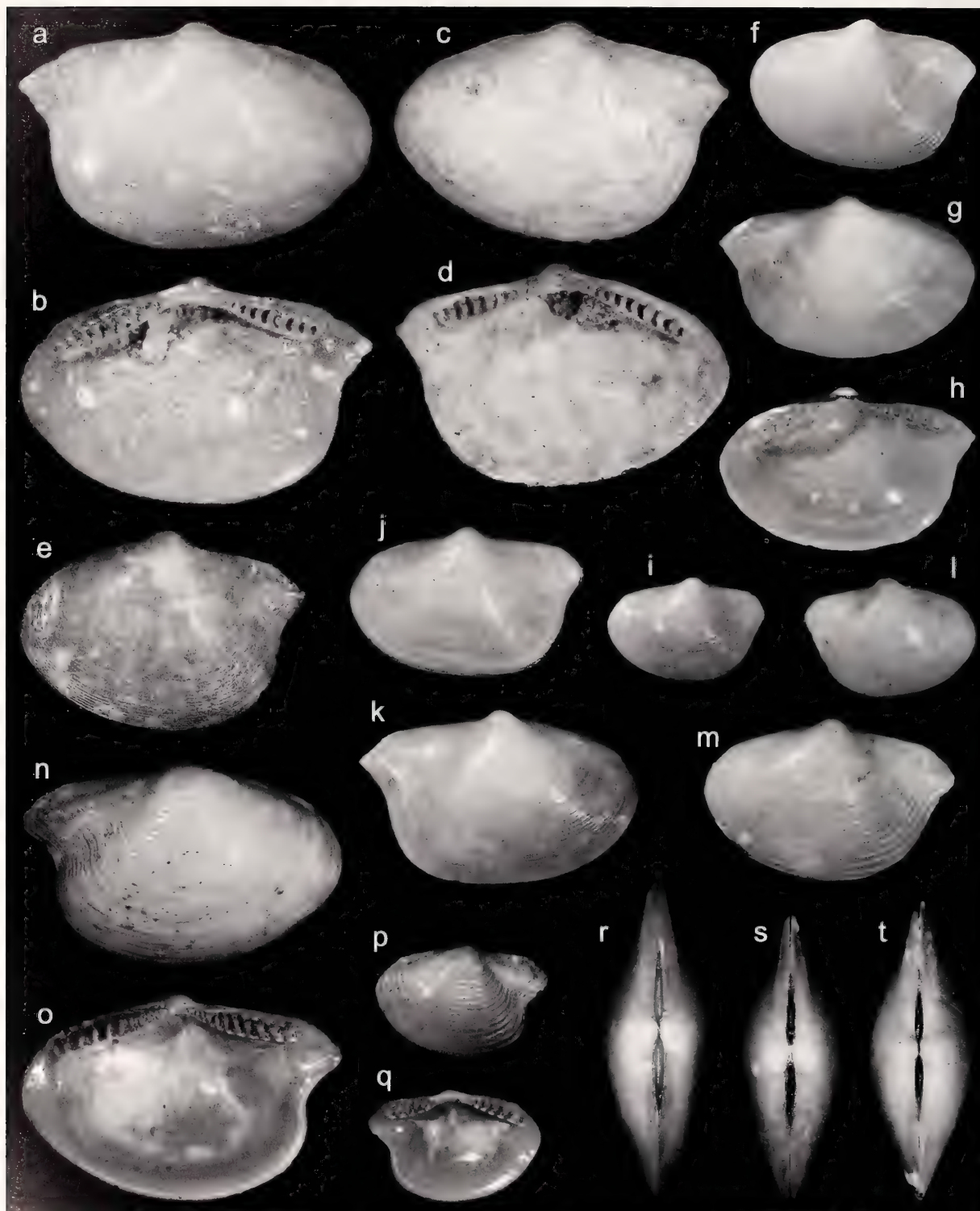


Figure 8. a–k. *Bathyspinula subexcisa* (Dautzenberg & Fischer, 1897). a, b. Syntype, length 6.81 mm, IRScN 1238/01. c, d. Syntype, length 6.52 mm, IRScN 1238/01. e. Syntype, length 5.47 mm, IRScN 1238/01. f. Challenger exp. (1973), st. 4, length 4.44 mm, MCZ 348787. g, h. Challenger exp. (1973), st. 4, length 5.01 mm, MCZ 348787. i. Challenger exp. (1973), st. 4, length 3.09 mm, MCZ 348787. j. Chain 106 exp., st. 318, length 4.42 mm, MCZ 348785. k. Chain 106 exp., st. 318, length 5.35 mm, MCZ 348785. l, m. *Bathyspinula hilleri* (Allen & Sanders, 1982). l. St. DS23, length 3.42 mm, MCZ 348807. m. St. DS23, length 4.93 mm,

less convex ventral margin (Figures 8j, k), but apparently without any clear-cut separation from the specimens with a more convex ventral margin.

The larval shell of *B. subexcisa* is ovate, similar in size and shape to that of *B. excisa* (Di Geronimo & La Perna, 1996:pl. 2, fig. 3), 280–300 µm in length, both in the type material and in the material from MCZ. This contrasts with the size of 450 µm reported by Allen & Sanders (1982:23): such a difference must be due to a measurement error.

Bathyspinula hilleri was described from the Angola Basin and reported from a number of stations through the Atlantic Ocean (Allen & Sanders, 1982). Some material (Figures 8m, t) from the West European Basin (st. DS23, 46°32.8'N, 10°21'W, no data on cruise and station depth, not reported by Allen & Sanders, 1982, tab. 4), matches the original description. It differs from *Bathyspinula subexcisa* by having a more convex ventral margin, a slightly coarser sculpture, particularly near the ventral margin, and by being slightly more inflated.

Bathyspinula excisa is notably common in the Plio-Pleistocene bathyal deposits cropping out in Italy (Di Geronimo & La Perna, 1996, 1997; La Perna, 2003). The finding of a single, fresh valve in the Ibero-Moroccan Gulf (Salas, 1996) seems to bring evidence that small populations are still present in the adjacent Atlantic. The depth range of *Bathyspinula excisa* was (or is) much shallower, from 200–300 m down to some 1000 m at least, than that of *B. subexcisa* and the other congeners, greatly exceeding 1000 m (Knudsen, 1970; Allen & Sanders, 1997; Olabarria, 2005).

Family Tindariidae Verrill & Bush, 1897

Genus *Tindaria* Bellardi, 1875

Tindaria perrieri (Dautzenberg & Fischer, 1897)

(Figures 9a–c)

Malletia perrieri Dautzenberg & Fischer, 1897:208, pl. 6, figs 15, 16.

Malletia perrieri var. *curta* Locard, 1898:333, pl. 18, figs 20–24.

Malletia perrieri – Dautzenberg, 1927:296, pl. 8, figs 19, 20.

Types: Monaco exps., st. 698 (*Princesse-Alice* 1896, st. 69), 39°11'N, 30°44'40"W, 1846 m, 1 v, MOM 21159, holotype.

Distribution: Azores (south-east of Flores) and North-west Africa (off Rabat), 1846–2190 m.

Remarks: The holotype is a poorly preserved right valve, somewhat robust, ovate in shape, with anterior and posterior ends well rounded and a strongly anterior umbo. Most of the outer surface bears only growth striae and ill-defined commarginal ridges, becoming better defined, sharper and regularly spaced towards the ventral margin. The hinge is moderately strong, arched with a continuous series of teeth. As observed by Dautzenberg & Fischer (1897), there is no ligament pit. A thin, barely visible external ligament furrow is present posteriorly, slightly extending anteriorly.

Malletia perrieri var. *curta*, described by Locard (1898) from the *Talisman* st. 16, 2190 m, off Rabat, Morocco (the original coordinates were based on the Paris meridian and the corrected version is 34°01'N, 08°32'W; S. Gofas, pers. comm.) is a synonym of *Malletia perrieri*. This is supported by the close matching of the two descriptions and the almost perfect overlap of the shell outlines. Locard's var. *curta* was said to be slightly higher and shorter, but the two original valves (of the same shell, as inferred from the illustrations) are only slightly larger, 9 mm in length, 8 mm in height, than the holotype of *Malletia perrieri* (7.93 × 6.92 mm), with the same length to height ratio.

According to Sanders & Allen (1977), *Tindaria* Bellardi, 1875 and *Pseudotindaria* Sanders & Allen, 1977 (currently in the Neilonellidae) cannot be distinguished from each other conchologically (*Pseudotindaria* differs from *Tindaria* by having siphons). Warén (1989) remarked that *Pseudotindaria* has an edentulous gap in the hinge, as in the type species *Pseudotindaria erebus* (Clarke, 1959). This observation seems more useful for distinguishing the two genera than the assumption by Maxwell (1988) that *Tindaria* lacks a pallial sinus. The type species of *Tindaria* is *T. arata* Bellardi, 1875, from the Late Miocene of the Turin area. The examination of the types and of abundant topotypic material of *T. arata* confirmed Warén's (1989:255, figs 19c, d) observations: 1) the tooth series is continuous (more precisely, there is a short interruption, sometimes poorly defined, much shorter than the edentulous gap in *Pseudotindaria*); 2) the pallial line is feeble, slightly distinct anteriorly, fading posteriorly and, apparently, without sinus.

The characters of *Malletia perrieri* all point to *Tindaria* (except for the inability to examine the pallial

MCZ 348807. n–q. *Bathyspinula excisa* (Philippi, 1844). n, o. Archi, southern Calabria, Early-Middle Pleistocene, length 6.21 mm, author's coll. p, q. Archi, southern Calabria, Early-Middle Pleistocene, length 3.25 mm, author's coll. r, s. *Bathyspinula subexcisa*. s. Same as Figure k. t. Challenger exp. (1973), st. 4, length 4.70 mm, MCZ 348787. t. *Bathyspinula hilleri*, same as Figure m.

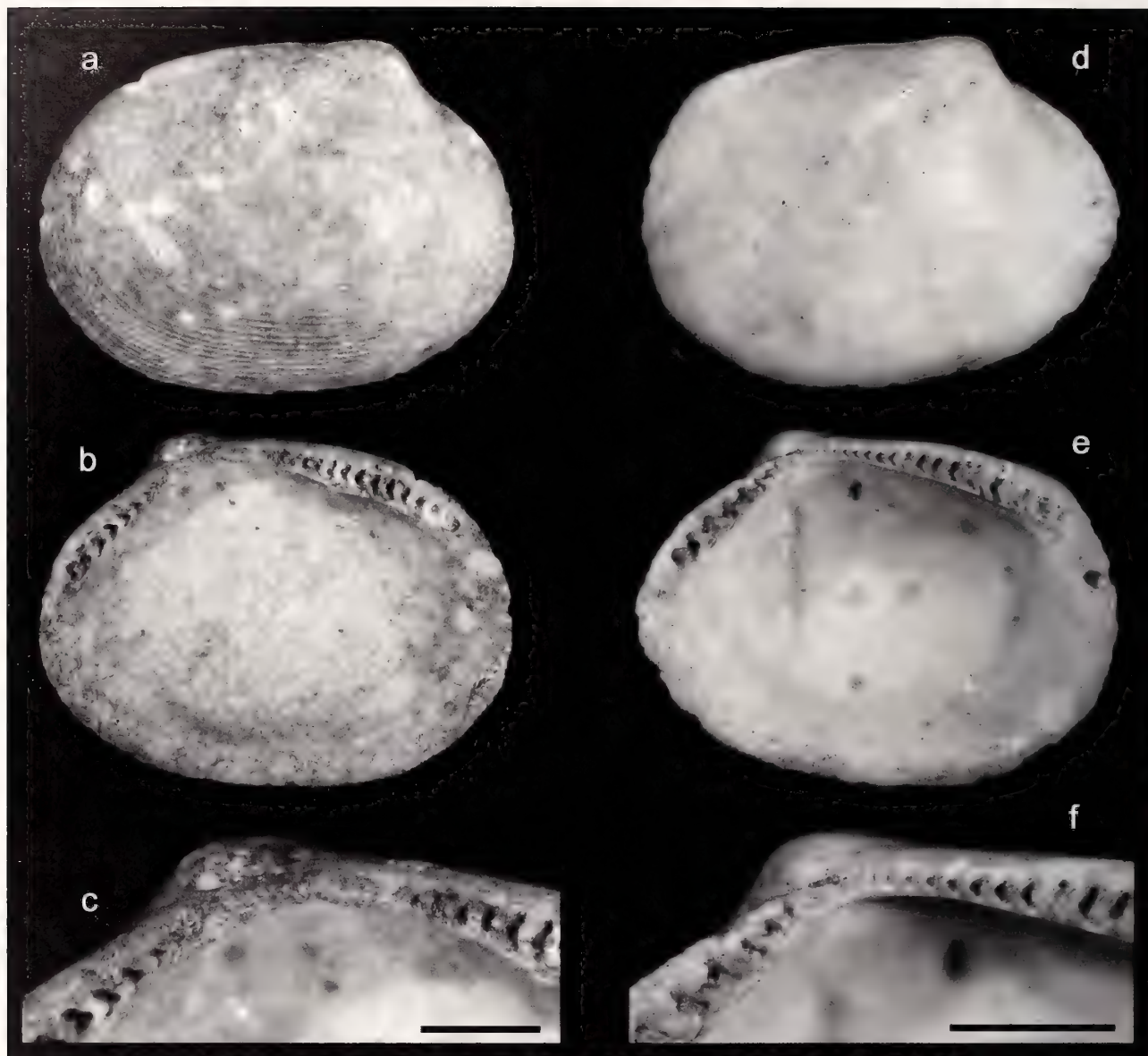


Figure 9. a–c. *Tindaria perrieri* (Dautzenberg & Fischer, 1897), holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 15, 16), length 7.93 mm, MOM 21159. d–f. *Tindaria* sp., length 5.96 mm, IRScN 1238/4. Scale bars = 1 mm.

line because of the poor preservation status). None of the Atlantic tindariids (Sanders & Allen, 1977; Warén, 1989) seems particularly similar to *Tindaria perrieri*.

A single right valve labelled as *Malletia perrieri* is present at IRScN (Figures 9d–f), from the same station as the holotype at MOM. No mention of this valve was made, either by Dautzenberg & Fisher (1897) or by Dautzenberg (1927). It is rather robust, not markedly convex, with a sculpture of only growth striae. The posterior margin is poorly convex or somewhat truncate, with a slope break at the postero-dorsal transition. An external ligament furrow is present

posteriorly. The pallial line is somewhat straight posteriorly, with no pallial sinus. It seems to represent an undescribed species, of uncertain systematic position, provisionally kept as *Tindaria* sp.

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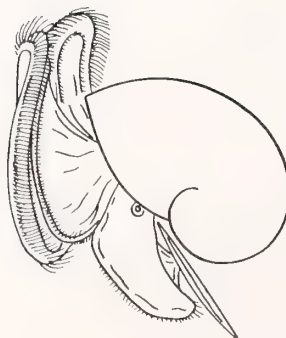
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Pliocene and Pleistocene *Fissurella* Bruguière, 1789 (Gastropoda: Fissurellidae) from Southern Peru

THOMAS J. DeVRIES 129

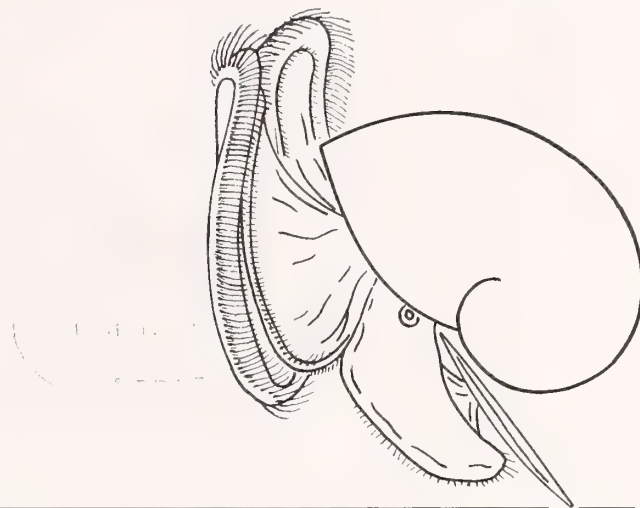
Revision of the Protobranch Species Described by Dautzenberg & Fischer (1897) with Description of a New Species and Taxonomic Comments on *Bathyspinula* (Bivalvia, Nuculanoidea)

RAFAEL LA PERNA 149



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CONTENTS

- Valiguna flava* (Heynemann, 1885) from Indonesia and Malaysia: Redescription and Comparison with *Valiguna siamensis* (Martens, 1867) (Gastropoda: Soleolifera: Veronicellidae)
SUZETE RODRIGUES GOMES, JULIANE BENTES PICAÑO, MENNO SCHILTHUIZEN AND JOSÉ WILLIBALDO THOMÉ 163
- Review of the Genera *Ividia*, *Folinella*, *Oscilla*, *Pseudoscilla*, *Tryptichus* and *Peristichia* (Gastropoda, Pyramidellidae) from Brazil, with Descriptions of Four New Species
ALEXANDRE D. PIMENTA, FRANKLIN N. SANTOS AND RICARDO S. ABSALÃO 171
- Galba truncatula* Müller, 1774 (Pulmonata: Lymnaeidae) in Argentina: Presence and Natural Infection by *Fasciola hepatica* (Linnaeus, 1758) (Trematoda: Digenea)
LAURA ISSIA, SILVIA M. PIETROKOVSKY, FLORENCIA KLEIMAN, PABLO CARMANHAHI AND CRISTINA WISNIVESKY-COLLI 185
- Diel Patterns of Vertical Distribution in Euthecosomatous Pteropods of Hawaiian Waters
DANIEL T. NIGRO AND ROGER R. SEAPY. 190
- Two New Species of *Doriopsilla* from the Tropical Western Atlantic with Remarks on *Cariopsillidae* Ortea & Espinosa, 2005
ÁNGEL VALDÉS AND JEFF HAMANN. 210
- Dendropoma mejillonensis* sp. nov., a New Species of Vermetid (Caenogastropoda) from Northern Chile
ALDO PACHECO AND JÜRGEN LAUDIEN. 219

CONTENTS — Continued

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Valiguna flava (Heynemann, 1885) from Indonesia and Malaysia:
Redescription and Comparison with *Valiguna siamensis* (Martens, 1867)
(Gastropoda: Soleolifera: Veronicellidae)

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Abstract. We redescribe and figure *Valiguna flava*, an almost unknown Southeast-Asian land slug. Detailed morphology, radula, jaw and living specimens of *Valiguna flava* were studied for the first time, based on material recently collected in Borneo and on the holotype. *Vl. flava* is also compared with *Valiguna siamensis*, the only other species of the genus, which is for the first time recorded in China.

Key Words: Morphology, anatomy, land slug, Borneo, Australasian region.

INTRODUCTION

Veronicellidae Gray, 1840 includes a large number of species of land slugs totally without shell (Thomé et al., 2006). Currently, 27 generic taxa are recognized for the family, which are distributed widely in the humid tropics and subtropics (Hoffmann, 1925; Forcart, 1953; Thomé, 1975; Gomes & Thomé, 2004). For the Oriental and Australian regions, Gomes & Thomé (2004) recognized six different genera (total of 13 species): *Filicaulis* Simroth, 1913, *Laevicaulis* Simroth, 1913, *Sarasinula* Grimpe & Hoffmann, 1924, *Semperula* Grimpe & Hoffmann, 1924, *Valiguna* Grimpe & Hoffmann, 1925 and *Veronicella* Blainville, 1817.

Originally, the taxon *Valiguna* was proposed by Grimpe & Hoffmann (1925a) as a subgenus of *Semperula* to include *Vaginula schneideri* Simroth, 1895 from Eastern Sumatra (Indrapura, Tandjong Kuba). However, in the same year that Grimpe & Hoffmann (1925a) proposed the taxon *Valiguna*, they rejected it and considered *Vaginula schneideri* a subspecies of *Semperula siamensis* (Martens, 1867) (Hoffmann, 1925; Grimpe & Hoffmann, 1925b). Only later, when Hoffmann (1941) found specimens which

he considered a new species very close to *Vaginula schneideri* (*Vl. isseli* Hoffmann, 1941), he reconsidered *Valiguna*, this time as a genus. Hoffmann (1941) included in *Valiguna*, *Vl. schneideri* and *Vl. isseli*, species in which the vas deferens does not open terminally (*acrocaulis* form, such as species of *Sarasinula*) nor basally in the penis (*pleurocaulis* form, such as species of *Semperula*), having an intermediate form, the *acropleurocaulis* or *pseudopleurocaulis* form.

Recently, Gomes & Thomé (2004) examined the holotype of *Vaginula flava* Heynemann, 1885 (considered by Hoffmann, 1925 a synonym of *Semperula maculata*) and also the original and subsequent descriptions of *Vl. schneideri* and *Vl. isseli* (Simroth, 1895; Grimpe & Hoffmann, 1925a, b; Hoffmann, 1925, 1941). They concluded that these three species are synonyms and that *Valiguna flava* is the valid name since it has priority. Gomes & Thomé (2004) also proposed the inclusion of *Semperula siamensis* into the genus *Valiguna* because this species also has an *acropleurocaulis* penis. According to Gomes & Thomé (2004), *Vl. flava* has records from Nias, Borneo and Indrapura (Indonesia), and *Valiguna siamensis* from Galle (Sri Lanka) and Petshaburi (Thailand). Both

species were insufficiently described in the original description. *Vaginulus reticulatus* Westerlund, 1883, which is a synonym of *Vl. siamensis* according to Gomes & Thomé (2004), was redescribed by Thomé (1984), although *Vl. flava* has not been studied since then.

Our primary purpose is, for the first time, to describe and figure in detail the morphology, radula, jaw, and living specimens of *Valiguna flava*. The study is based on samples recently collected from Borneo and on the holotype. The species is also compared with *Valiguna siamensis*, the only other species of the genus, based on material from China and on the paratypes of *Vaginulus reticulatus* (synonym of *Vl. siamensis*).

MATERIAL AND METHODS

Six living and adult specimens of *Vl. flava*, which were collected in Borneo and deposited in the Museum BORNEENSIS of Universiti Malaysia Sabah, were analyzed. The holotype and paratype of this species, deposited in the Natural History Museum (BMNH-1880.10.6), London, England were also studied.

Vl. flava was also compared with four specimens of *Vl. siamensis* deposited in the Museum of the Institute of Zoology, Chinese Academy of Sciences, Beijing (China) (lots ZMIZ01091, ZMIZ01092), from Yunnan and Guangxi, China. The type-material of *Vaginulus reticulatus* Westerlund, 1883 (13 specimens) (synonym of *Vl. siamensis* according to Gomes & Thomé, 2004), deposited at Swedish Museum of Natural History (Stockholm, Sweden) was also examined (lots SMNH 6427, SMNH 3753).

The specimens of both species were dissected under a stereomicroscope for studying the internal structures. Drawings were done using a camera lucida. Two jaws and two radulae (from each species) were extracted under the stereomicroscope and later analyzed using a scanning electron microscope (SEM Philips XL 30).

The terminology used and the morphological and anatomical characteristics described and illustrated are those usually considered diagnostic in the Veronicellidae (Hoffmann, 1925; Coifmann, 1935; Forcart, 1953; Barker, 2001; Thomé et al., 2002; Gomes & Thomé, 2001, 2004).

Valiguna flava (Heynemann, 1885)

(Figures 1–12)

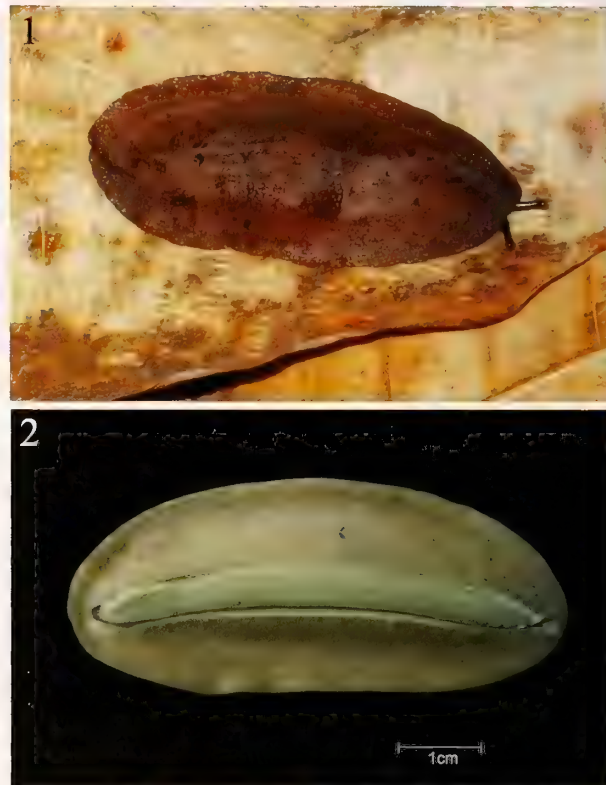
Vaginula flava Heynemann, 1885:10–11.

Vaginula schneideri Simroth, 1895:7–8.

Semperula (Valiguna) schneideri; Grimpe & Hoffmann 1925a: 391–392.

Semperula siamensis schneideri; Hoffmann, 1925: 181–182; Grimpe & Hoffmann, 1925b:18–19, 31–33.

Valiguna schneideri; Hoffmann, 1941:236.



Figures 1–2. External characteristics of *Valiguna flava*. 1, dorsal position of a living specimen (BOR/MOL 3411); 2, ventral position of a fixed specimen (BOR/MOL 3439).

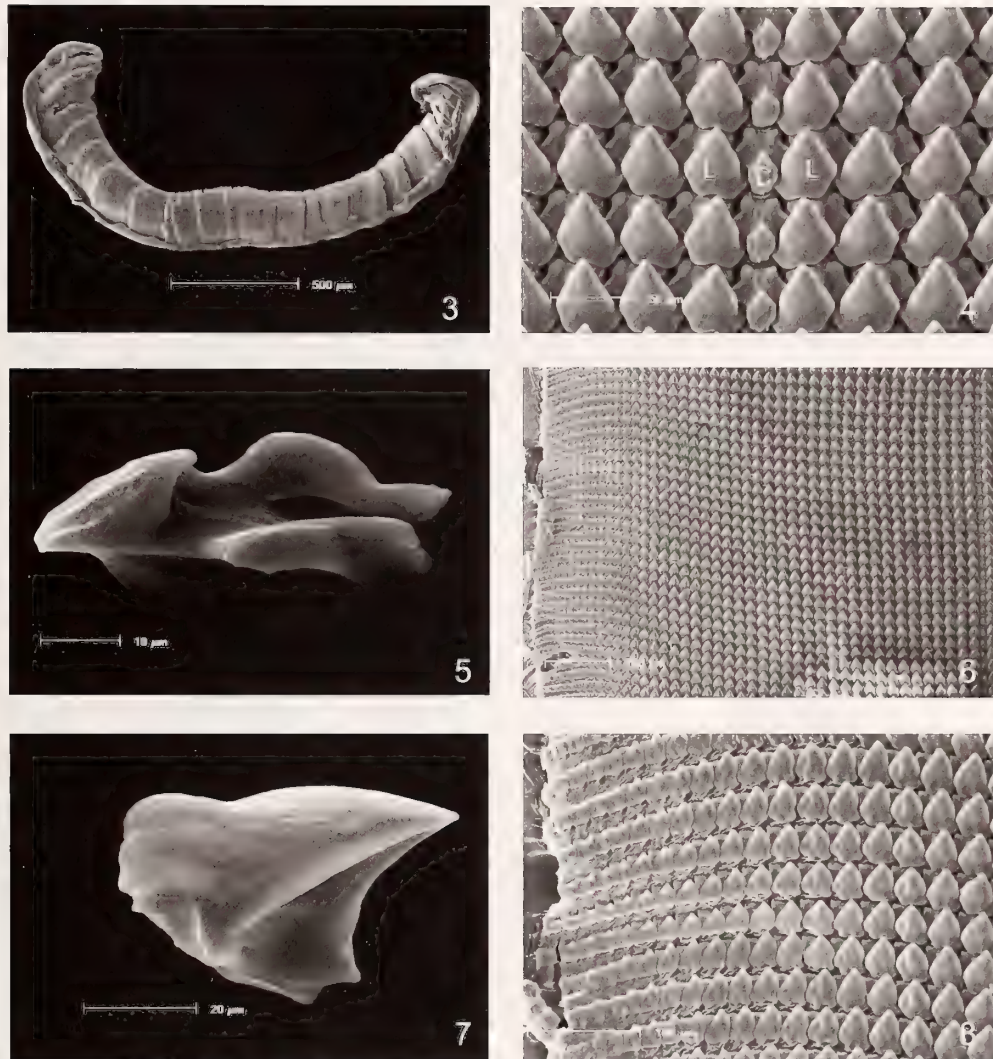
Valiguna isseli Hoffmann, 1941:234.

Diagnostic Features

The main diagnostic structure in Veronicellidae is the penis. The penis of *Valiguna flava* has a glans and a base completely distinct from each other. The base is a cylindrical structure, without peculiarities in outer surface. The glans starts from a flap that surrounds the distal extremity of the penis base. First, it is cylindrical, but then it curves, forming a peak, in whose extremity the vas deferens opens. In the dorsum of the curvature (penis apex) is a cylindrical structure covered by dentate and serrated formations (Figures 9–12).

External Characteristics

The specimens are relatively large and they have an oval body (Figures 1–2). The notum (dorsal region) is smooth only with some widely spaced granules. There are some scattered blackish spots and also a narrow light line on the dorsum (Figure 1). This last one is in the middle of the notum and is not always clearly visible. The notum ground coloration ranges from pale



Figures 3–8. Radula and jaw of *Valiguna flava* (BOR/MOL 3409). 3, entire jaw; 4, lateral (L), central (C) and lateral (L) teeth, respectively; 5, lateral view of a central tooth; 6, medium part of the right half of the radula; 7, lateral view of a lateral tooth; 8, lateral teeth in the edges of the radula.

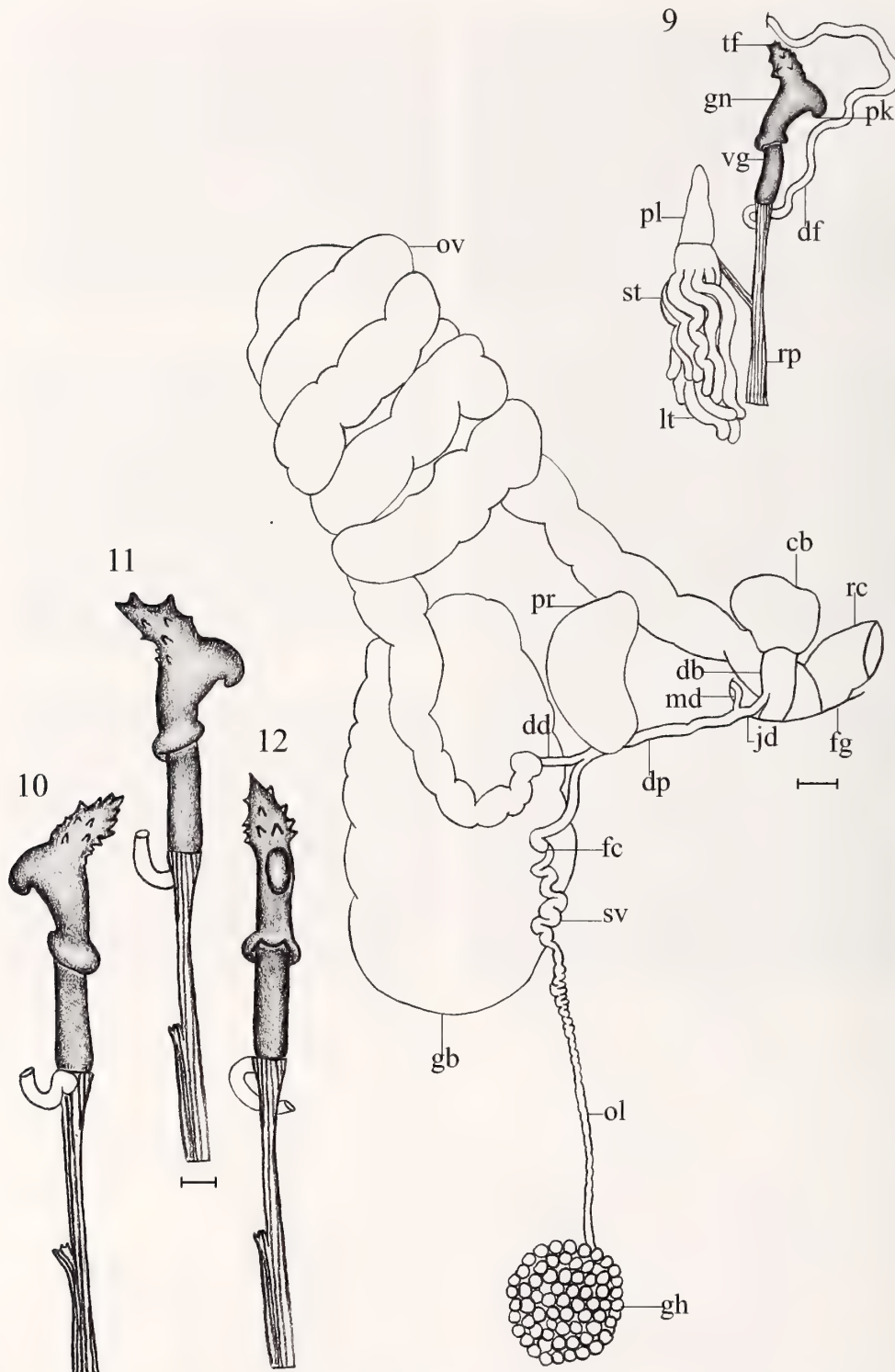
yellowish brown to dark reddish brown. The hyponotum is also pigmented from pale yellowish brown to dark reddish brown, depending of the notum coloration. However, it is always much lighter than the notum and has a homogeneous coloration, without spots or lines or only with few tiny blackish spots (Figure 2). The sole is light beige and very narrow, having less than half of the hyponotum width. The female pore is situated at ca. 45% of the length of the body measured from the front, and it is far from the pedal groove by ca. $2/5$ the width of the hyponotum. In all specimens the female pore is surrounded by a slender line of black pigmentation (Figure 2).

Holotype measurements (mm): body length (70.00), body width (29.00), sole width (5.44) and hyponotum width (8.11). Measurements (mm) (6 other specimens):

body length (45–60), body width (22–30), sole width (2.5–4.8) and hyponotum width (5.2–10.5).

Digestive System

The mouth is followed by a buccal bulb (= pharynx), where the radula and the jaw lie. There are two salivary glands with very slender, ramified and delicate acini connected to the buccal bulb. The buccal bulb is connected to the esophagus, which is followed by the gastric crop. The latter is barely delimited from the esophagus, both having almost the same diameter. The gastric crop leads into a stomach, which is long (twice longer than wide). Two lobules of the digestive gland open into the stomach, one anterior and another one posterior. The anterior lobe does not totally cover the



Figures 9-12. Reproductive system in *Valiguna flava* (BOR/MOL 3409). 9, complete reproductive system; 10-12, three different positions of the penis (cb, bursa copulatrix; db, duct of the bursa copulatrix; dd, distal posterior deferens; df, vas deferens; dp, proximal posterior deferens; fc, fertilization complex; fg, female genital pore; gb, albumen gland; gh, hermaphroditic gland; gn, glans; jd, canalis junctor; lt, long tubules; md, middle deferens; ol, spermi duct; ov, oviduct; pk, peak, in whose extremity the deferens opens; pl, penial gland papilla; pr, prostate; rc, rectum; rp, penis retractor muscle; st, short tubules; sv, seminal vesicle; tf, structure covered by dentate and serrated formations; vg, penis base. Scale bar: 1 mm.

anterior intestinal loop. The intestine starts from the stomach, follows to the anterior region where it forms a loop (the anterior intestinal loop) and then continues back to the posterior region. Near the height of the female pore, the intestine penetrates in the body wall, where the rectum begins. The rectum continues to the end of the body where it opens via the anus. The latter is located centrally in the body and is totally hidden over the sole. The anal opening is represented by a fissure. Neither a circular opening (with a defined border) nor an opercular membrane is found. The anal opening floor is formed by well developed folds that sometimes seem papillae. The nephridium does not have an external aperture. It is probably connected to the rectum within the body wall.

The jaws are well arquated and narrow. They are formed by an average of 24 wide and superposed ribs. The three ribs of the middle are somewhat higher and less distinct from the others (Figure 3).

The radula has 93–95 teeth per transverse row, which is formed by one symmetrical central or rhachis tooth (Figures 4–5), flanked on both sides by 46–47 lateral teeth (Figures 6–7). The dental formula is $C/1+L46-47/2$. The lateral teeth are smaller towards the edges of the radula (Figure 8).

Pedal and Pallial Nerves, Pedal Aortic System

One pair of pallial and one of pedal nerves run from the central nervous system towards the posterior extremity of the body cavity (Barker, 2001). They are parallel and together from the central nervous system until near the height of the bursa copulatrix. After, they are parallel but separated from each other and run like that until the end of the body cavity. The pedal aortic artery begins at the level of the central nervous system and runs between the nerves (centrally) until around the level of the bursa copulatrix.

Pedal Gland

The pedal gland, located on the anterior extremity of the sole under the head, is short and straight. It is broad in its proximal portion (in the aperture), narrowing in the middle and with the posterior extremity rounded and somewhat broadened (producing a goblet-shape). It has two different areas: one external lighter and one internal yellowish. The posterior extremity of the gland receives a wide pedal gland artery (Coifmann, 1935).

Reproductive System

The bursa copulatrix (= spermatheca or gametolitic gland) is almost circular, but somewhat concave in the middle. It has a cylindrical duct a little longer than the

bursa copulatrix. The canalis junctor (Barker, 2001; Gomes & Thomé, 2004) penetrates in the duct of the bursa copulatrix, near to the half of the total length of the duct. The oviduct is wider near to the female genital pore, involving the duct of the bursa copulatrix (Figure 9).

The penis has a glans and a base well differentiated. The base of the penis is somewhat cylindrical and smooth. The glans starts from an surrounding structure (as a flap) at the distal extremity of the penis base; it is initially cylindrical and smooth, but quickly tapers and curves forming a peak, in whose extremity the vas deferens opens. In the dorsum of the curvature is a cylindrical structure covered by dentate and serrated formations, which is in the distal extremity of the penis (Figures 9–12).

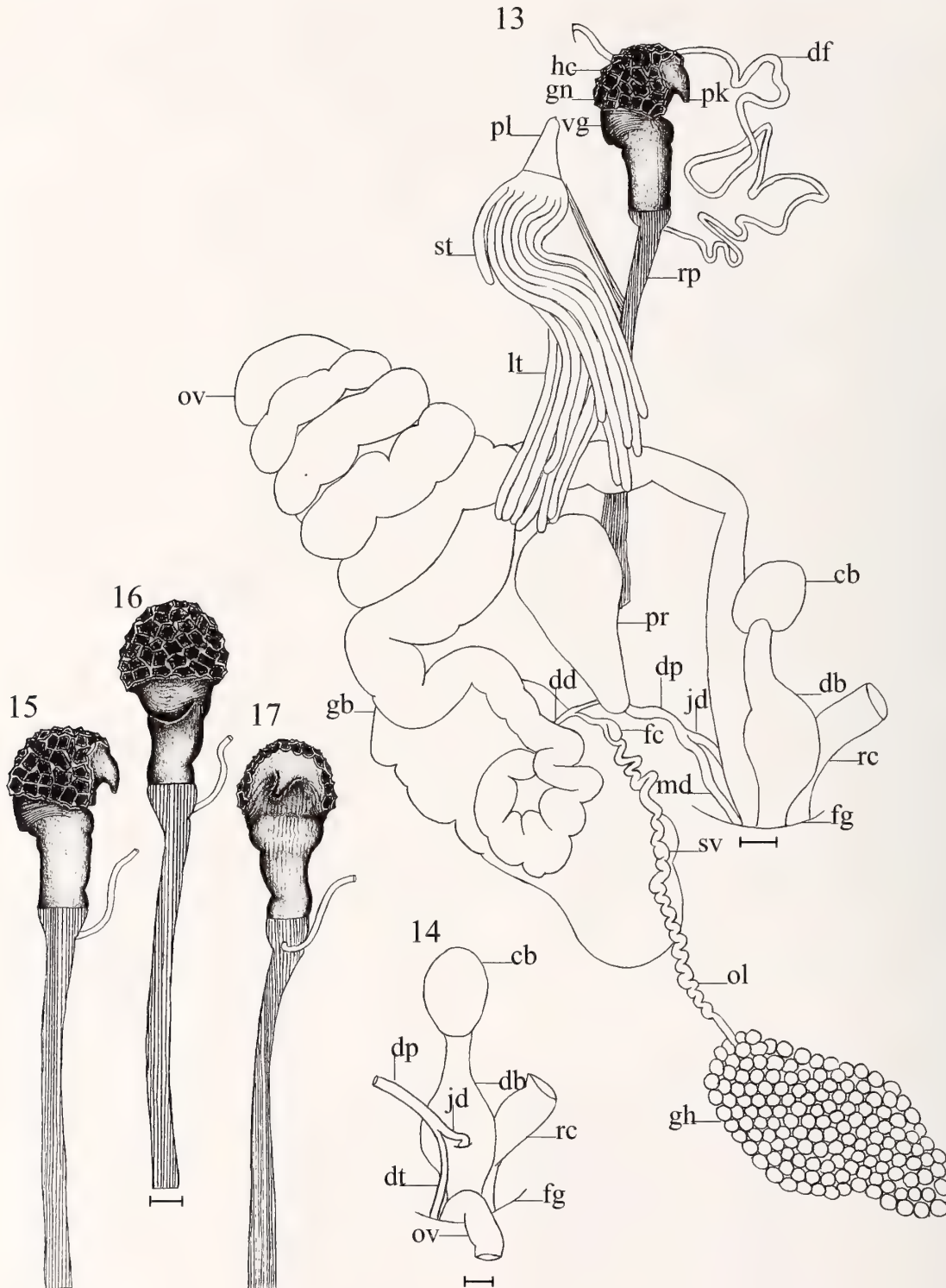
The penial gland is small and has a length similar to the length of the penis. It is formed by a papilla and by about 15 short tubules (they exceed a little the height of the pericardium). The papilla is relatively long, with around half of the tubules' length. The tubules are not differentiated in groups according to length, although subtle differences in tubule lengths is observed.

Distribution: Islands of Sumatra and Borneo (Fig. 18).

Natural history: They were found on the forest floor, at night and early in the morning, in one case more or less clustered around a rotten log.

Type-material: Holotype. INDONESIA, **Borneo:** P. E. Gerrard col. (BMNH 1880.10.6.4). Other materials. MALAYSIA, **Sabah:** Danum Valley Field Centre, ca. 60 km W of Lahad Datu, primary dipterocarp forest, ca. 300 m asl. (04°58'00"N 117°48'00"E), 2 specimens, 2003.80.W, P. Craze & M. Schilthuizen col. (BOR/MOL 3409); Danum Valley Borneo Rainforest Lodge, 1 specimen, 2000.84.W, C. Rutjes col. (BOR/MOL 3410); Kota Kinabalu Distr., Poring Hot Springs, 660 m asl. (06°02'87"N 116°42'16"E), 1 specimen, 2001.59.W, M. Schilthuizen & P. Koomen col. (BOR/MOL 3411); Interior Prov., Tenom (behind Perkasa Hotel), 327–400 m asl. (05°07'17"N 115°56'40"E), 1 specimen, 2003.89.W, M. Schilthuizen col. (BOR/MOL 3438); Kinabalu National Park (Poring Hot Springs), 500 m asl., 1 specimen, 2003/03/24 (2003.26.W), M. Schilthuizen col. (BOR/MOL 3439).

The lot deposited at Natural History Museum in London (England) (BMNH 1884.1.10.1), which is identified as a paratype of *Vl. flava*, is not *Vl. flava*. In this specimen (adult), that has not been dissected yet, the penis (the main diagnostic characteristic) is completely different. It is probably an unknown species of Veronicellidae.



Figures 13–17. Reproductive system in *Valiguna siamensis* (ZMIZ01092). 13, complete reproductive system; 14, detail of the bursa copulatrix; 15–17, three different positions of the penis (cb, bursa copulatrix; db, duct of the bursa copulatrix; dd, distal posterior deferens; df, vas deferens; dp, proximal posterior deferens; fc, fertilization complex; fg, female genital pore; gb, albumen gland; gh, hermaphroditic gland; gn, glans; hc, honeycomb aspect structure; jd, canalis junctor; lt, long tubules; md, middle deferens; ol, oviduct; ov, oviduct; pk, peak, in whose extremity the deferens opens; pl, penial gland papilla; pr, prostate; rc, rectum; rp, penis retractor muscle; st, short tubules; sv, seminal vesicle; vg, penis base). Scale bar: 1 mm.

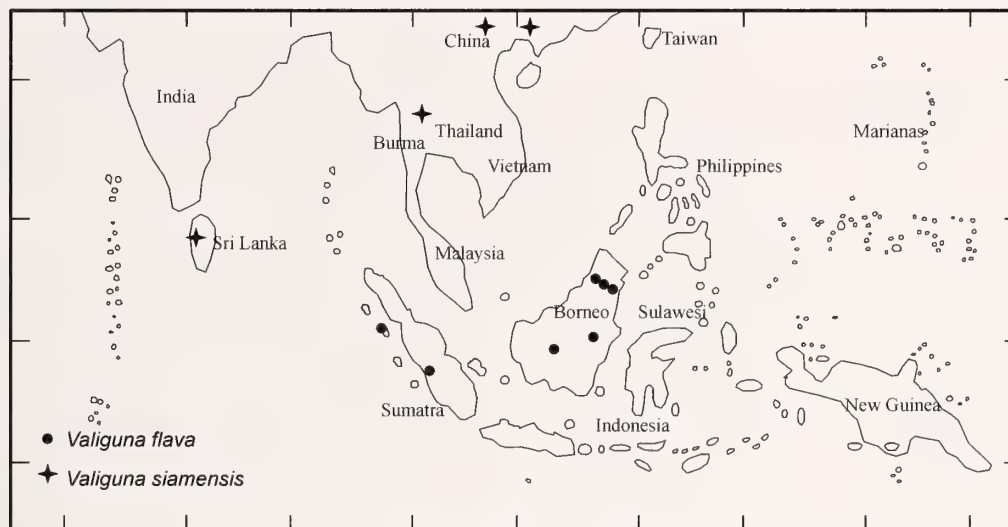


Figure 18. Map showing the distribution of *Valiguna flava* and *Valiguna siamensis*, considering bibliography records and the lots recently collected in the north of Borneo and China.

DISCUSSION

Vl. flava and *Vl. siamensis* are clearly close species. They share several morphological characteristics, although important differences are also found between them.

The penis is the structure that most notably discriminates *Vl. flava* from *Vl. siamensis* and even from the other species of the family. The dentate and serrated formation found in the distal extremity of the penis of *Vl. flava* is very characteristic and it is found only in this species of Veronicellidae. In *Vl. siamensis*, the vas deferens also opens in a lateral peak and a well developed base is found. But, in this species the penis has a formation like a “honeycomb” located in the distal extremity (Figures 13–17). It is a complex structure, which is practically absent in juvenile specimens. The bursa copulatrix region has also some differences. In *Vl. siamensis*, the bursa copulatrix duct is extended in the medium region, assuming a domed aspect. In *Vl. siamensis* the bursa duct is fairly longer than the copulatrix bursa, different from *Vl. flava*. In this species, the bursa is small and assumes a form from spherical to elliptical. In both species, the canalis junctor penetrates in the bursa copulatrix duct, not in the bursa itself (as in many other species of Veronicellidae).

The other internal characteristics are very similar between *Vl. flava* and *Vl. siamensis*. The characteristics of the digestive system as well as radula and jaw do not show significant differences between both species. Also the disposition of the pairs of pedal and pallial nerves and pedal aortic system are the same in *Vl. flava* and *Vl. siamensis*. The pedal gland is also similar. Moreover, all the other described characteristics regarding

on the reproductive system (as copulatrix bursa region and penial gland) are very similar between both species.

The body form differs between *Vl. flava* and *Vl. siamensis*. The first one has an oval body while the other is longer and narrower, although in both species the sole width is smaller than half the width of the right hyponotum. Unfortunately, the coloration can not be compared since the specimens of *Vl. siamensis* from China were all completely discolored. The specimens of *Vs. reticulatus* examined by Thomé (1984), and again by us, were also discolored. Externally, *Vl. flava* can be identified mainly by presence of wide blackish spots in the notum, although there is some variation in the intensity of the notum ground coloration (Figure 1).

Vl. siamensis, previously redescribed by Thomé (1984) when he studied *Va. reticulatus* from Galle (synonyms), is recorded for the first time to China (Yunnan and Guangxi) (Figure 18).

Acknowledgements. We are grateful to Centro de Microscopia e Microanálises (CEMM) of Pontifícia Universidade Católica do Rio Grande do Sul for the SEM photomicrographs; to Peter Koomen for the photo of the living specimen; Suzete R. Gomes, Juliane Picanço and José W. Thomé gratefully acknowledges financial support from “Conselho Nacional de Desenvolvimento Científico e Tecnológico.” Menno Schilthuisen gratefully acknowledges financial support from the Royal Netherlands Embassy, Kuala Lumpur.

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Review of the Genera *Ividia*, *Folinella*, *Oscilla*, *Pseudoscilla*, *Tryptichus* and *Peristichia* (Gastropoda, Pyramidellidae) from Brazil, with Descriptions of Four New Species

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Abstract. The taxonomy of the species belonging to the genera *Ividia* Dall & Bartsch, 1904, *Folinella* Dall & Bartsch, 1904, *Oscilla* A. Adams, 1961, *Pseudoscilla* Boettger, 1901, *Tryptichus* Mörch, 1875 and *Peristichia* Dall, 1889 from Brazil is reviewed. The following species are reported: *Ividia havanensis* (Pilsbry & Aguayo, 1933), *Folinella robertsoni* (Altena, 1975), *Pseudoscilla babylonica* (C. B. Adams, 1845), *Peristichia agria* Dall, 1889, *Oscilla somersi* (Verrill & Bush, 1900) and *Tryptichus niveus* Mörch, 1875; the last two species are for the first time recorded from Brazil. Four new species are described: *Tryptichus litosbathron* n.sp. is characterized by its smooth base; *Oscilla notialis* n.sp. and *Oscilla aquilonia* n.sp. differ in the degree of projection of the protoconch nucleus, and both species are closely related to *Oscilla tornata* (Verrill, 1884), differing in details of spiral sculpture; and *Peristichia lepta* n.sp. is distinguished from other *Peristichia* species by its slender shell, absence of a columellar fold, and by the numerous spiral cords on the base.

Key Words: Mollusca, Pyramidellidae, Odostomiinae, taxonomy, Brazil, *Ividia*, *Folinella*, *Oscilla*, *Pseudoscilla*, *Tryptichus*, *Peristichia*.

INTRODUCTION

The family Pyramidellidae from Brazil is the subject of a major taxonomic review that has already yielded some published results (Pimenta et al., 2000; Pimenta & Absalão 2001a, 2001b, 2002, 2004a, 2004b; Absalão et al., 2003), in addition to others in preparation. In each of these papers, selected genera were studied, commonly resulting in amendments to the taxonomic status of pyramidellid species reported from Brazil, as well as revealing several new species and expanding the geographic distributions for known species in the Western Atlantic. In this paper we deal with the Odostomiinae and Pyramidellinae genera *Ividia* Dall & Bartsch, 1904, *Folinella* Dall & Bartsch, 1904, *Oscilla* A. Adams, 1861, *Pseudoscilla* Boettger, 1901, *Tryptichus* Mörch, 1875 and *Peristichia* Dall, 1889.

The supraspecific classification of the family Pyramidellidae is controversial. There is no consensus about the status of most of the more than 300 generic or subgeneric names (Schander et al., 1999). Particularly, in most genera of the subfamily Odostomiinae,

the characters of the shell overlap somewhat, and clear differences cannot be established. While some authors (e.g., Dall & Bartsch 1904, 1909; Abbott 1974; Diaz & Puyana 1994) consider the genus *Odostomia* in a very broad sense, with many subgenera, others have been using many of these subgenera at full generic rank, giving rise to narrower definitions of each genus. Many of these genera have been interpreted differently in several studies in different geographic areas (e.g., Robertson 1978; Jong & Coomans 1988; Linden & Eikenboon 1992; Schander 1994; Peñas et al., 1996; Peñas & Rolán 1998; Redfern 2001, among others), often giving rise to different generic allocations for the same species. We believe that a consensus will be reached only after more detailed studies, including the careful comparison of type species, and eventually adding anatomical or molecular data.

Our goal, in this paper, is not to provide precise definitions for supraspecific taxa, but rather a more taxonomically accurate knowledge of the diversity and geographic range of the Brazilian pyramidellid fauna. In most cases, we adopted a conservative option,

following previous allocations of the species herein studied, thus avoiding new combinations. It should be clear, then, that most of the generic allocations used herein are to be considered provisional and changes based on new evidence are to be expected in the future.

Abbreviations used: –Collections: ANSP - Academy of Natural Sciences of Philadelphia, Philadelphia, USA; Col.Mol.UERJ - Coleção de Moluscos da Universidade do Estado do Rio de Janeiro; CR - collection Colin Redfern; DOUFPE - Departamento de Oceanografia da Universidade Federal de Pernambuco, Recife; IBUFRJ - Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MNHN - Muséum National d'Histoire Naturelle, Paris; MNRJ - Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro; MZSP - Museu de Zoologia da Universidade de São Paulo, São Paulo; USNM - National Museum of Natural History, Washington, DC; YPM - Peabody Museum of Natural History / Yale University, New Haven; ZMA - Zoologisch Museum Amsterdam, Amsterdam; –Expeditions: AMASSEDs - A Multidisciplinary Amazon Shelf Sedimentary Study, Research Vessel "Columbus Iseling" Coll.; GEOMAR XII - Comissão Oceanográfica Geologia Marinha XII, NOAS Coll.; MD55 - Marion Dufresne Expedition; PADCT - Programa de Apoio ao Desenvolvimento Científico e Tecnológico, Research Vessel "Professor W. Besnard" coll.; REVIZEE - Recursos Vivos da Zona Econômica Exclusiva, Research Vessel "Professor W. Besnard" coll. (except when noted); –Collectors: AG - Research Vessel "Astro Garoupa," Petrobras SA; Eq. Zoo Coll. - equipe do Departamento de Zoologia, IBUFRJ; NOAC - Research Vessel "Almirante Câmara," Marinha do Brasil; NOAN - Research Vessel "Antares," Marinha do Brasil; NOAS - Research Vessel "Almirante Saldanha," Marinha do Brasil.

MATERIAL AND METHODS

The determination of the material was based on comparisons against type material and/or original descriptions and illustrations. In the material examined lists, the number inside brackets indicates the number of shells in each lot. This report is based entirely on empty shells from Brazilian and foreign collections. All lots from MNHN were collected along the northeast Brazilian coast by P. Maestrati from 1984 to 1989.

SYSTEMATICS

Subfamily Odostomiinae Pelseener, 1928

Genus *Ividia* Dall & Bartsch, 1904

Ividia Dall & Bartsch, 1904: 11. Type species: *Parthenia armata* Carpenter, 1857, Mazatlan, by original designation.

Ividia havanensis (Pilsbry & Aguayo, 1933)

(Figure 1A–E)

Odostomia (Miralda) *havanensis* Pilsbry & Aguayo, 1933: 118, pl. 6, fig. 4; Odé & Speers (1972: 9, not illustrated); Abbott (1974: 298, fig. 3627); Vokes & Vokes (1983: 32, pl. 30, fig. 12); Diaz & Puyana (1994: 235, pl. LXIX, fig. 934).

Miralda havanensis: Olsson & McGinty (1958: 44, pl. 1, fig. 8); Rios (1970: 134, 1975: 143, pl. 43, fig. 665, 1985: 165, pl. 54, fig. 784, 1994: 188, pl. 62, fig. 877); Jong & Coomans (1988: 124, pl. 6, 26, fig. 651); Mello (1990: 40, fig. 9); Barros (1994a: 74, not illustrated).

Ividia havanensis: Redfern (2001: 144, pl. 65, fig. 595).

Type material: Holotype ANSP 159722.

Type locality: La Chorrera, Habana, Cuba.

Material examined: Pará state: IBUFRJ 13693, AMASSEDs sta 3228, [1]; –Rio Grande do Norte state: DOUFPE 5012, sta 17 (05°01.317'S / 36°23.507'W, 9.1 m), 05/iiiiv/2002, [1]; DOUFPE 5013, sta 30 (04°47'30.837"S / 36°40'02.678"W, 17.3 m), 27/vii/2002, [1]; –Pernambuco state: IBUFRJ 11153, Ilha Rata, Fernando de Noronha Archipel, 08/vii/1999, [3]; MNHN, Cabo (enseada dos corais), [16]; MNHN, Cabo (praia de Gaibu), [12]; MNHN, São Luiz (areia preta) Maranhão, [3]; MNHN, Paulista (Maria Farinha), [2]; MNRJ 10822, Paulista (praia da Conceição), [2]; MNHN, Recife (praia do Pina), [2]; MNHN, environs de Recife, [6]; MNHN, Cabo (Pedras Pretas), [8]; MNHN, Paulista (praia da Conceição), [1]; –Sergipe state: DOUFPE 5011, sta 9.2 (11°30'08"S / 37°07'56"W, 1031 m), 19/iv/2002, [1]; –Bahia state: IBUFRJ 6374, off Abrolhos, 1990, [3]; –Espírito Santo state: IBUFRJ 8573, off Camburi, 1993, [15]; IBUFRJ 8998, off Aracruz, 18/xii/1989, [1]; IBUFRJ 8481, off Piúma, 1993, [1]; IBUFRJ 8656, off Piúma, 1993, [1]; –Rio de Janeiro state: Col.Mol.UERJ 1977, Enseada de Dois Rios, Ilha Grande, 19–20/xi/1996, [1]; Col.Mol.UERJ 3336, Ilha Grande sta 16 (Rochedo São Pedro, 23°2.868'S / 44°32.722'W, 10 m), [1]; Col.Mol.UERJ 3349, Ilha Grande sta 15 (Ponta Grande Timuiba, 23°3.762'S / 44°36.038'W, 7 m), [8]; IBUFRJ 13688, praia da Figueira, Angra dos Reis, 1998, [7]; –São Paulo state: MZSP 86785, PADCT sta 6577 (25°15.76'S / 45°04.62'W, 124 m), off São Paulo state [1].

Distribution: USA: Florida (Abbott 1974), Texas (Odé & Speers 1972); Caribbean: Habana, Cuba (Pilsbry & Aguayo 1933); Yucatan Peninsula, Mexico (Vokes & Vokes 1983); Panama (Olsson & McGinty 1958); Colombia (Diaz & Puyana 1994); Bahamas (Redfern 2001); Aruba, West Indies (Jong & Coomans 1988); Brazil: Atol das Rocas and Alagoas (Rios 1994);

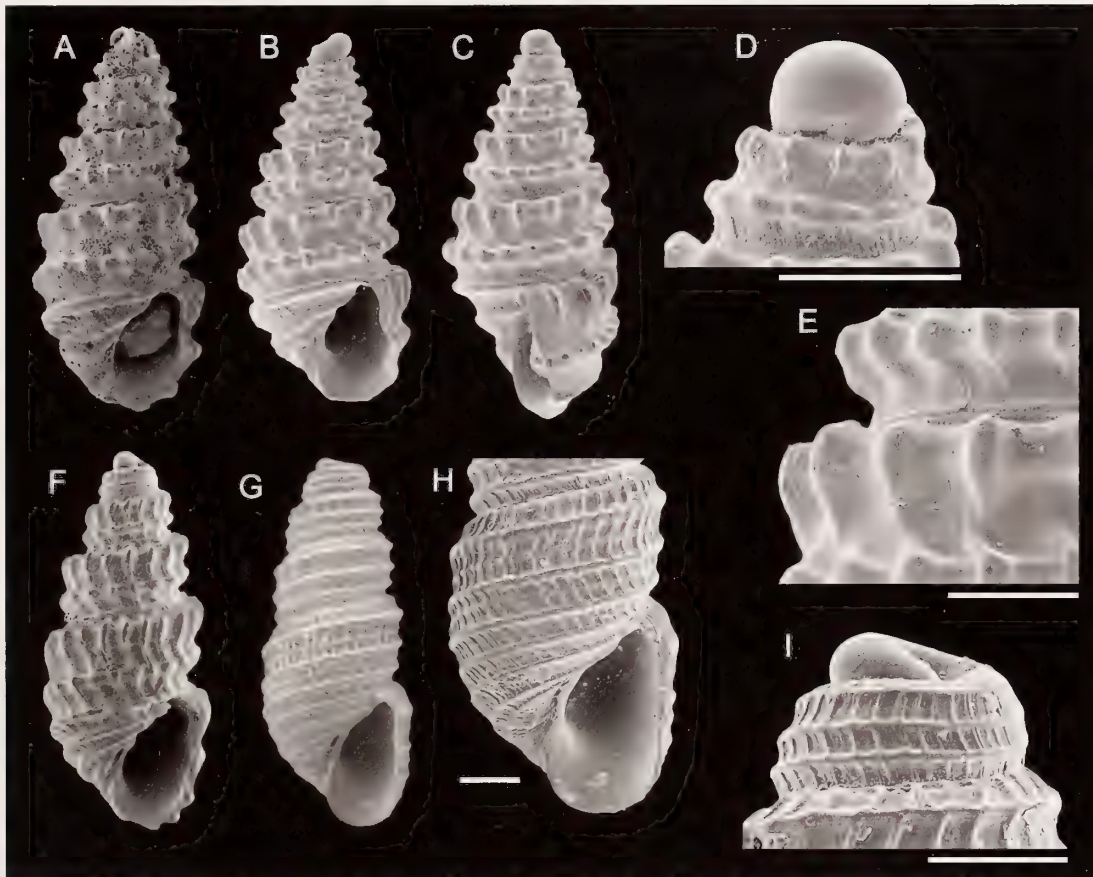


Figure 1. A–E, *Ividia havanensis* (Pilsbry & Aguayo, 1933): A, holotype (ANSP 159722); B, E, MNRJ 10822; C–D, Col.Mol.UERJ 1977. A–C, whole shells (respective lengths: 1.9 mm; 1.7 mm; 1.7 mm); D, protoconch; E, detail of last whorl; F, holotype of *Ividia abbotti* (Olsson & McGuinty, 1958) (ANSP 211912, length: 2.0 mm); G–I, *Folinella robertsoni* (Altena, 1975) (MNRJ 10823): G, whole shell (length: 1.6 mm); H, last whorl; I, protoconch. Scale bars: 200 μ m.

Canopus, Ceará (Barros 1994a); Pernambuco (Mello 1990; this study); Pará, Rio Grande do Norte, Fernando de Noronha Archipel, Maranhão, Sergipe, Bahia, Espírito Santo, Rio de Janeiro and São Paulo (this study).

Remarks: The genus *Ividia* was proposed by Dall & Bartsch (1904) as a subgenus of *Odostomia*. This taxon was later synonymized under *Miralda* A. Adams, 1863 by Dall & Bartsch (1909, p. 172), who argued that the type species that they selected for *Ividia* (*Parthenia armata* Carpenter, 1857) should be referred to *Miralda*.

Ividia havanensis (Figure 1A–E), *Ividia abbotti* (Olsson & McGuinty, 1958) (Figure 1F) and also *Folinella robertsoni* (see discussion below) were, in fact, included in *Miralda*, as a full genus (Olsson & McGinty 1958; Altena 1975; Rios 1994; Jong & Coomans 1988) and as a subgenus of *Odostomia* (Pilsbry & Aguayo 1933; Odé & Speers 1972; Abbott 1974; Vokes & Vokes 1983; Diaz & Puyana 1994).

Although Schander et al. (1999) adopted the synonymy between *Miralda* and *Ividia*, Odé (1993),

on the other hand, considered that *Parthenia armata* is not congeneric with the type species of *Miralda* (*Parthenia diadema* A. Adams, 1860), and therefore considered *Ividia* a valid genus. This position was followed by Turgeon et al. (1998) and Redfern (2001).

In fact, the illustration of *Miralda diadema* provided by Dall & Bartsch (1906, pl. XVII, fig. 2) is quite distinct from the illustration of *Ividia armata* by Dall & Bartsch (1909: pl. 19, fig. 6). *Ividia armata* has a conical shell with two strong nodulose spiral cords in each teleoconch whorl, and weaker spiral cords on the base; whereas *Miralda diadema* has a somewhat globose shell with a pattern of axial ribs and spiral cords forming nodules where they cross. We, therefore, follow Odé (1993) in considering *Ividia* a valid genus.

Considering *Ividia* valid, Odé (1993) included *Ividia abbotti*; Redfern (2001) included *Ividia havanensis* and *Ividia robertsoni*. However, while we agree with Odé (1993) and Redfern (2001) in regard to *I. abbotti* and *I. havanensis*, we propose the new combination *Folinella robertsoni* (see below). We consider that the shell of the

latter differs considerably from typical *Ividia* species, in having three spiral cords in each whorl, crossed by thin axial ribs, lacking the nodulose spiral cords (Figure 1G–H), which fits well with the description of *Ividella* by Dall & Bartsch (1909: 172–174, pl. 18, figs. 11, 11a).

Lia decorata Folin, 1873 was referred to *Miralda* by Odé & Speers (1972: 9) and may prove to be an additional species of *Ividia*, because the shell also has the nodulose spiral cords. Faber (1988) stated that “*Odostomia havanensis* Pilsbry & Aguayo, 1933 = *Lia decorata* De Folin, 1873,” but provided no further discussion on this possible synonymy. The illustration provided by de Folin (1873: pl. 6, fig. 8) indeed resembles *I. havanensis*, but has a shell with spiral nodules very close to each other and with more rounded summits.

Besides the records from the east coast of the U.S.A. and the Caribbean, *Ividia havanensis* was listed and illustrated from Brazil by Rios (1994), in the genus *Miralda*; however, Rios provided no illustrations of specimens from Brazil, but reproduced the original figure. Other records from Brazil include those of Mello (1990) and Barros (1994a), from two localities on the northeast coast. We now present records of this species from nearly the entire Brazilian north, northeast and southeast coast, considerably enlarging its known geographic range in the Western Atlantic, to about 25°S.

Genus *Folinella* Dall & Bartsch, 1904

Folinella Dall & Bartsch, 1904: 10, *nom. nov. pro* *Amoura* de Folin, 1873 *non* *Amoura* Forbes, 1845.

Type species: *Amoura anguliferens* de Folin, 1873, by monotypy.

Folinella robertsoni (Altena, 1975)
new combination

(Figure 1G–I)

Miralda robertsoni: Altena (1975: 75, fig. 30a–b); Mello (1990: 40, fig. 8); Rios (1994: 188, pl. 62, fig. 878); Barros (1994b: 44, fig. 12a).

Odostomia (*Miralda*) cf. *robertsoni*: Diaz & Puyana (1994: 235, pl. LXIX, fig. 935).

Ividia robertsoni: Redfern (2001: 144, pl. 65, fig. 596).

Type locality: Shell ridge near Cupido on the Maratukka, Nickerie District, Suriname.

Material examined: Rio Grande do Norte state: DOUFPE 5015, sta 01 (05°04.260'S / 36°20.303'W, 3.6 m), 06/viii/2002, [2]; –Pernambuco state: MNHN, Paulista (Maria Farinha), [19]; MNHN Cabo (praia de Gaibu), [10]; MNRJ 10823 Paulista (praia da Conceição), [5]; MNHN Cabo (enseada dos corais), [8]; MNHN Raposa (praia de Raposa), [15]; MNHN Itamaracá (praia de Jaguaribe), [1]; MNHN Recife

(praia de Candeias), [8]; MNHN Recife (praia do Pina), [8]; MNHN Recife (praia do Pina), [11]; –Maranhão state: MNHN São Luiz (areia preta), [5]; –Espírito Santo state: IBUFRJ 10856, Baía de Vitória, 18/xii/1998, [2]; –Rio de Janeiro state: IBUFRJ 7477, off Arraial do Cabo, 1993, [2]; Col.Mol.UERJ 3340, Ilha Grande sta 15 (Ponta Grande Timuiba, 23°3.762'S / 44°36.038'W, 7 m), [2]; Col.Mol.UERJ 3351, Ilha Grande sta 15 (Ponta Grande Timuiba, 23°3.762'S / 44°36.038'W, 7 m), [2]; IBUFRJ 13689, Angra dos Reis (praia da Figueira), 1998, [4].

Distribution: Suriname (Altena 1975); Caribbean: Colombia (Diaz & Puyana 1994); Bahamas (Redfern 2001); Brazil: Pernambuco, Maranhão (Mello 1990; Barros 1994b; this study); Rio Grande do Norte; Espírito Santo; Rio de Janeiro (this study).

Remarks: The taxonomy and nomenclature of *Folinella* were discussed by Aartsen (1984), Aartsen et al. (1998) and Schander et al. (1999), who considered it as a senior synonym of *Ividella* Dall & Bartsch, 1909. As demonstrated by Aartsen (1984), the type species of *Folinella* is *Amoura anguliferens*. This genus is characterized by numerous axial and two to three spiral ribs, equally strong and forming small knobs at their crossings; this sculpture invades the base of the shell. The same pattern of sculpture can be found in some of the species listed by Dall & Bartsch (1909) in the genus *Ividella*, which should thus be referred to *Folinella* (e.g., *F. quinquecincta* Carpenter, 1856, *F. delmontensis* Dall & Bartsch, 1907, *F. navisa* Dall & Bartsch, 1909, *F. araniiana* Dall & Bartsch, 1909).

The species herein included in *Folinella* was considered to belong in *Miralda*, as a full genus (Altena, 1975; Mello, 1990; Rios, 1994; Barros, 1994b) or as a subgenus of *Odostomia* (Diaz & Puyana, 1994). Redfern (2001), on the other hand, used the combination *Ividia robertsoni*.

The new combination *Folinella robertsoni* is proposed herein based on similarities to the concept of *Folinella*, as adopted by Aartsen et al. (1998). *Folinella robertsoni* has three spiral cords in each whorl, crossed by thin axial ribs, with small nodulose spiral cords (Figure 1G–I), which fits well within the concept of *Folinella* (fide Aartsen et al., 1998).

Folinella robertsoni was listed and illustrated by Rios (1994), in the genus *Miralda*. He provided no illustrations of specimens from Brazil, but reproduced the original figure, and recorded the range of the species in Brazil as “northeast.” Other records from northeastern Brazil are those of Mello (1990) and Barros (1994a). The present paper enlarges the known geographic range of *F. robertsoni* in the Western Atlantic up to about 23°S, on the coast of Rio de Janeiro.

Genus *Oscilla* A. Adams, 1861

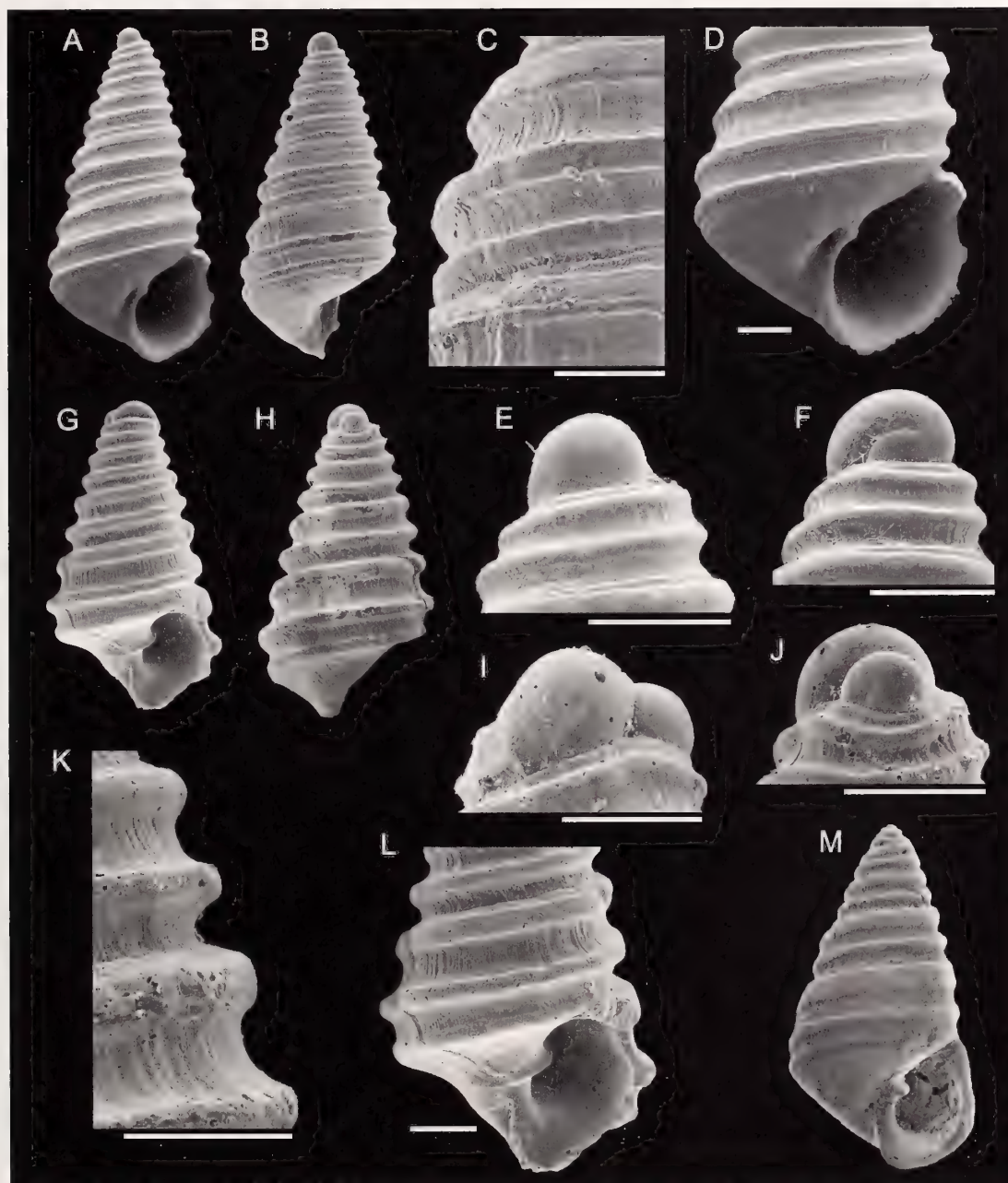


Figure 2. A–F, *Oscilla notialis* n.sp.: A–E, holotype (MNRJ 10692); F, paratype (IBUFRJ 7595); A–B, whole shell (length: 1.9 mm); C, detail of sculpture on last whorl; D, Last whorl; E–F, protoconch; G–L, *Oscilla aquilonia* n.sp.: holotype (MNRJ 10825); G–H, whole shell (length: 1.53 mm); I–J, protoconch; K, detail of sculpture on last whorl; L, last whorl; M, holotype of *Oscilla tornata* (Verrill, 1884) (USNM 30083). Scale bars: 200 μ m.

Oscilla A. Adams, 1861. Type species: *Monoptygma* (*Oscilla*) *cingulata*.

Oscilla notialis n.sp.

(Figure 2A–F)

Type material: Holotype: MNRJ 10692, off Sergipe

state, sta 2.1 (11°23'21"S / 37°04'30"W, 99 m), 16/iv/2002. Paratypes: –Sergipe state: IBUFRJ 14077, type locality [3]; DOUFPE 5000, type locality, [9]; DOUFPE 5006, sta 2.3 (11°24'14"S / 37°05'08"W, 99 m), 16/iv/2002, [2]; –Espírito Santo state: IBUFRJ 14082, off Espírito Santo state, REVIZEE Central I sta D1 (20°48'72"S / 41°09'33"W), 23/ii/1996, [1]; –Rio de Janeiro state: IBUFRJ 12316, Cabo Frio VII sta 6194,

off Rio de Janeiro state, iii/1983, [2]; MNHN, Cabo Frio VII sta 6194, off Rio de Janeiro state, iii/1983, [3]; IBUFRJ 9627, Arquipélago de Santana sta 2, Macaé, 3–5/v/1993, AG coll., [1]; IBUFRJ 6934, off Rio de Janeiro state, GEOMAR XII sta 89 (21°47.8'S / 40°16'W), 28/viii/1979, [3]; IBUFRJ 7595, off Rio de Janeiro state, GEOMAR XII sta 76 (21°57'S / 40°51'W), 28/viii/1979, [2]; MZSP 86791, PADCT sta 6617 (21°51.6'S / 47°42'W, 327 m), off Rio de Janeiro state [5]; –São Paulo state: MZSP 89799, REVIZEE sta 6662 (24°00.95'S / 43°55.54'W, 135 m), [11]; MNRJ 10942, REVIZEE sta 6669 (24°7.42'S / 44°42.22'W, 101 m), [8]; MZSP 86792, PADCT sta 6571 (24°12.74'S / 44°58.98'W, 79 m), [29]; MZSP 86800, REVIZEE sta 6666 (24°17.13'S / 44°12.15'W, 163 m), [1]; MZSP 86797, PADCT sta 6579 (24°42.302'S / 45°18.831'W, 84 m), [1]; MZSP 86787, PADCT sta 6573 (24°42.608'S / 44°43.419'W, 155 m), [1]; MZSP 86794, PADCT sta 6577 (25°15.76'S / 45°04.62'W, 124 m), [14]; MZSP 86788, PADCT sta 6541 (26°15'S / 45°53'W, 130 m), [5]; –Paraná state: MZSP 86790, PADCT sta 6631 (25°46'S / 45°28.8'W, 164 m), [2]; –Santa Catarina state: MZSP 86798, PADCT sta 6595 (26°23.55'S / 46°39.49'W, 175 m), [9]; MZSP 86801, PADCT sta 6641 (26°15'S / 45°53'W, 130 m), [1]; MNHN, REVIZEE sta 6695 (26°17.134'S / 46°41.788'W, 153 m), [3]; MZSP 86793, PADCT sta 6606 (27°48.07'S / 47°24.04'W, 175 m), [1]; MZSP 86795, PADCT sta 6635 (27°10.38'S / 47°27.54'W, 129 m), [2].

Type locality: off Sergipe state coast (11°23'21"S / 37°04'30"W, 99 m).

Distribution: Only known from Brazil. Northeast coast: Rio Grande do Norte and Sergipe states; southeast and south coasts: Espírito Santo, Rio de Janeiro, São Paulo, Paraná and Santa Catarina states.

Etymology: From the Latin *notialis*: southern. Referring to the main distribution area of this species, in southern latitudes off Brazil.

Diagnosis: *Oscilla* species with planispiral heterostrophic protoconch; strongly conical shell bearing wide spiral cords and grooves in teleoconch whorls, and an additional, narrower spiral cord above the suture, variably expressed.

Description: Shell conic, holotype 1.9 mm in length. Teleoconch with up to 5 whorls with crenulated outline. Suture deep. Protoconch heterostrophic planispiral, with about 1.5 whorls, smooth, forming an angle of about 90° to shell main axis, diameter about 200 µm. Spiral sculpture formed by three cords: the widest cord just above the suture; a second cord of medium width in the middle of each whorl; and a third, narrower cord just above the suture, partially covered by the subsequent whorl, almost inconspicuous in early

whorls; between the cords, there are two wide spiral furrows with microscopic axial growth lines. Base slightly convex, with microscopic axial ribs and with its adapical periphery marked by a peripheral, smooth spiral cord that corresponds to the third spiral cord in the teleoconch whorls, and bordered adapically by two additional, very thin spiral cords; with a chink-like umbilicus. Aperture rhomboid, with a columellar fold somewhat projected. Outer lip thin and slightly crenulated.

Oscilla aquilonia n.sp.

(Figure 2G–L)

Type material: Holotype: MNRJ 10825, off Pará state, AMASSEDs sta 3228 (03°25.1'N, 49°56.4'W, 64 m), 17/v/1990, RVCi coll. Paratypes: IBUFRJ 4169, type locality, [1]; IBUFRJ 14895, type locality, [3]; MNHN, type locality, [2]; MNRJ 10819, type locality, [3]; IBUFRJ 14897, off Pará state, AMASSEDs sta 4134, RVCi coll., [1].

Type locality: off Pará state, north Brazilian coast - AMASSEDs sta 3228 (03°25.1'N, 49°56.4'W, 64 m).

Distribution: Only known from Pará state, north Brazil.

Etymology: From the Latin *aquilonius*: north. Referring to the occurrence of this species on the northern coast of Brazil.

Diagnosis: *Oscilla* species with helicoid heterostrophic protoconch with strongly projected nucleus; conical shell bearing wide spiral cords and grooves in teleoconch whorls, and an additional, narrower spiral cord above the suture, variably expressed.

Description: Shell conic, holotype 1.14 mm in length. Teleoconch with up to three whorls, with crenulated outline. Suture deep. Protoconch heterostrophic helicoid, with about 1.5 whorls, well projected, smooth, forming an angle of about 90° to shell main axis, diameter about 200 µm. Spiral sculpture formed by three cords: the widest cord just above the suture; a second cord, of medium width in the middle of each whorl; and a third, narrower cord, just above the suture, partially covered by the subsequent whorl, almost inconspicuous in early whorls; between the cords, there are two wide spiral furrows with microscopic axial growth lines. Base slightly convex, with microscopic axial ribs and with its adapical periphery marked by a peripheral, smooth spiral cord that corresponds to the third spiral cord in the teleoconch whorls; with a small chink-like umbilicus. Aperture rhomboid, with a columellar fold, medium projected. Outer lip thin and slightly crenulated.

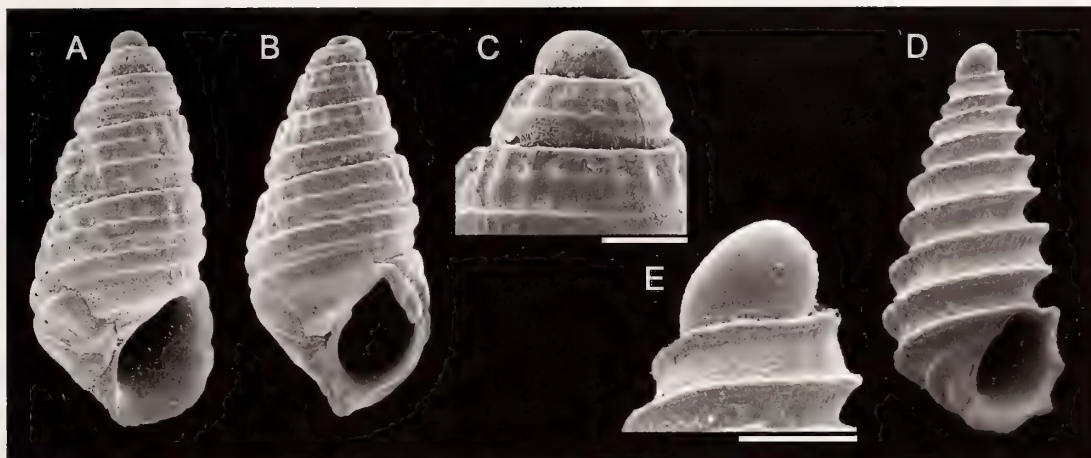


Figure 3. A–C, *Oscilla somersi* (Verrill & Bush, 1900) (IBUFRJ 13667): A–B, whole shells (respective lengths: 1.5 mm; 1.6 mm); C: protoconch; D–E, *Pseudoscilla babylonica* (C. B. Adams, 1845) (IBUFRJ 8490): D, whole shell (length: 1.6 mm); E, protoconch. Scale bars: 200 μ m.

Oscilla somersi (Verrill & Bush, 1900)
new combination

(Figure 3A–C)

Odostomia (*Evalea*) *somersi* Verrill & Bush, 1900: 533, pl. 65, fig. 7.

Miralda havanensis auct. non (Pilsbry & Aguayo, 1933): Sá et al. (1984: 7, fig. 41).

Menestho somersi: Jong & Coomans (1988: 124, pl. 6, fig. 652); Redfern (2001: 144, pl. 65, fig. 598A; pl. pl. 113, fig. 598B).

Boonea somersi: ? Odé (1993: 55, not illustrated).

Boonea someri (sic): Wise (2001: 74, not illustrated).

Type locality: Bermuda.

Material examined: Bahamas Islands: CR 3641, 26°39'N, 77°18'W, 0.3 m, 20/vii/1982 [5]; CR 10098, NE of Chub Rocks (26°44'N, 77°12'W, 23 m), 12.vii.1992 [1]; –West Indies: ZMA, Aruba, F. Verbene coll. [28]; ZMA, Curaçao, Jong coll. [2]; –Brazil: –Espírito Santo state: IBUFRJ 8689, off Piúma, [36]; –Rio de Janeiro state: IBUFRJ 13667, Praia da Figueira, Angra dos Reis, C. Alvarenga coll. [14]; MNHN, Praia da Figueira, Angra dos Reis, C. Alvarenga coll. [6]; MNRJ 10820, Praia da Figueira, Angra dos Reis, C. Alvarenga coll. [6]; coll. Mol. UERJ 5961, Ponta do Pinto, Enseada de Parati-Mirim (23°13.249'S / 44°38.950'W, 5 m), Ilha Grande Bay, [12]; coll. Mol. UERJ 6213, Ponta Grande Timuiba (23°3.762'S / 44°36.038'W, 9 m), Ilha Grande Bay, [22]; coll. Mol. UERJ 6244, Ponta Escalvada, Ilha da Gipóia (23°1.911'S / 44°22.734'W, 11 m), Ilha Grande Bay, [35]; coll. Mol. UERJ 6234, Ilha Comprida, Baía de Ribeira (23°57.724'S / 44°22'W, 9 m), Ilha Grande Bay

[17]; coll. Mol. UERJ 6256, Laje do Coronel (23°5.884'S / 44°24.410'W, 23 m), Ilha Grande Bay [15].

Distribution: USA: Texas (Odé 1993); Caribbean: Bermuda (Verrill & Bush 1900); Bahamas (Redfern 2001); Curaçao, West Indies (Jong & Coomans 1988); Brazil: southeast coast (this study).

Remarks: The genus *Oscilla* was proposed as subgenus of *Monoptygma* by A. Adams (1861) and diagnosed with elevate spiral cords, aperture subquadrate, with a columellar fold. Tryon (1886) used *Oscilla* as a section in the *Pyramidella* subgenus *Syrnola*. Van Aartsen (1994) used *Oscilla* as a full genus, recording *Oscilla jocosu* from Mediterranean. Schander et al. (1999) considered *Oscilla* as a genus in the subfamily Chrysallidinae.

The three species herein included in this genus fit well such diagnosis, with a conical shell, strong spiral cords and a distinctly visible columellar fold.

Other pyramidellid genera have a similar pattern of strong spiral cords, such as *Pseudoscilla*, *Cingulina* and *Menestho*. *Oscilla somersi* (new combination here proposed), for example, has already being allocated to the genus *Menestho* by Jong & Coomans (1988) and Redfern (2001). However, *Menestho* is a genus originally described based on *Turbo albulus* Fabricius, 1780, a species from Greenland. Also, *Oscilla somersi* was included in *Boonea* by Odé (1993) and Wise (2001), a position with which we do not agree, since *Boonea* has three nodulose spiral cords in each whorl.

The original figure of *Oscilla somersi* shows smooth spiral cords. In the shells from Brazil and the West Indies that we examined, we could find some variation in the first two spiral cords, which range from almost completely smooth to sculptured with small nodules of

varying strength. The shell illustrated by Redfern (2001) also bears somewhat nodulose spiral cords, but some variation in the spiral ridges also can be found (Redfern, personal communication). Odé (1993), although expressing doubts about his generic allocation, found variation in the spiral ridges too. According to Johnson (1989), the shells in a lot labeled as syntypes (YPM 15710) do not correspond to this species.

Oscilla notialis (Figure 2A–F) and *Oscilla aquilonia* (Figure 2G–L) differ from the holotype of *Oscilla tornata* Verrill, 1884 (new combination, herein proposed), from off Cape Hatteras, U.S.A. (Figure 2M), in respect to the very narrow upper spiral cord and wider spiral grooves between the cords. Furthermore, Verrill (1884) did not report an additional, narrower spiral cord above the suture, which is found in *Oscilla notialis* (Figure 2A–B) and also in very similar specimens from Abaco (Bahamas), named *Oscilla* sp. B by Redfern (2001: pl. 65, fig. 600), which may prove to be this species too. This additional spiral cord is a variable character, being stronger in some shells and absent in others. In *Oscilla aquilonia*, an additional, suprasutural cord may also be present, to a variable degree (Figure 2G, E).

Oscilla aquilonia is very similar to *Oscilla notialis*, but has a helicoid protoconch (Figure 2I–J), whereas *Menestho notialis* has a planispiral one (Figure 2E–F). Furthermore, *O. aquilonia* does not have the two thin spiral cords at the periphery of the last whorl and abapically adjacent to the suture, as seen in *O. notialis* (Figure 2C–D).

Oscilla notialis shows a wide range of variation, both in shell size (up to five teleoconch whorls) and ornamentation (spiral cords sometimes with subquadrate edges, and umbilicus wider in some shells). *Oscilla aquilonia*, on the other hand, is consistently smaller, with almost no variation in the above characters. In spite of the variation found in *M. notialis*, the protoconch is always planispiral (Figure 2E–F).

This is the first record of *Oscilla somersi* from the southwestern Atlantic, where it has been collected off the southeast Brazilian coast (about 23°S). *Oscilla notialis* has a wide range of distribution in Brazil, from the northeast (about 4°S) to the southeast coast (about 20°S). *Oscilla aquilonia*, on the other hand, was found only in northern localities (about 03°N).

Genus *Pseudoscilla* Böettger, 1901

Pseudoscilla Böettger, 1901. Type species: *Oscilla* (*Pseudoscilla*) *miocaenica* Böettger, 1901.

Pseudoscilla babylonica (C. B. Adams, 1845)

(Figure 3D–E)

Chemnitzia babylonica C. B. Adams, 1845: 6: Odé &

Speers (1972: 6, not illustrated); Clench & Turner (1950: 259, not illustrated)

Chemnitzia (*Miralda*) *babylonica*: Mörch (1875: 165, not illustrated).

Odostomia (*Cingulina*) *Babylonica*: Tryon (1886: 358, not illustrated).

Chemnitzia Babylonica: Bush (1899: 176, not illustrated).

Odostomia (*Cingulina*) *Babylonica*: Verrill & Bush (1900: 534, pl. LXV, fig. 11).

Menestho babylonica: Odé & Speers (1972: 8, not illustrated).

Odostomia (*Miralda*) *judithae* Newell-Usticke (1959: 86): synonymized by Jong & Coomans (1988).

Cingulina babylonica: Warmke & Abbott (1962: 148, not illustrated); Abbott (1974: 301, not illustrated); Rios (1985: 165, pl. 54, fig. 785, 1994: 188, pl. 62, fig. 876); Vokes & Vokes (1983: 32, pl. 30, fig. 19); Jong & Coomans (1988: 120, pl. 19, fig. 637); Mello (1990: 41, fig. 10).

Cingula babylonica: Oliveira (1992: 285, not illustrated).

Pseudoscilla babylonica: Odé (1993: 58, not illustrated).

Odostomia babylonica: Wise (1996: 445, figs. 13a–e); Redfern (2001: 142, pl. 64, fig. 585).

Type material: lost (Clench & Turner 1950)

Type locality: Jamaica.

Material examined: Pernambuco state: MNHN, Cabo (praia de Gaibu), [1]; –Bahia state: MNHN, Itaparica (praia do Vera Cruz), [1]; MNHN, MD55 sta DC73 (18°59'S / 37°48'W, 607–620 m), Abrolhos Archipel Continental slope, Bouchet, Leal, Metivier coll. [2], –Espírito Santo state: IBUFRJ 8490, off Piúma 1993, [3]; MNRJ 10821, off Piúma 1993 [1]; –Rio de Janeiro state: IBUFRJ 6975, GEOMAR XII sta 111, 29/viii/1979, NOAC coll., [1]; IBUFRJ 7071, Cabo Frio VII sta 6194 (24° 03,6' S / 044° 07,6' W, 134 m), iii/1983, NOAS coll., [1]; IBUFRJ 7836, GEOMAR XII sta 96 (22°05'S / 40°17,4'W), NOAC coll., [1].

Distribution: USA: Florida (Wise 1996), Texas (Odé 1993); Caribbean: West Indies (Jong & Coomans 1988), Bermuda (Verrill & Bush 1900), Bahamas (Redfern 2001); Brazil: Pernambuco state (Mello 1990; this study), Bahia (Oliveira 1992), Espírito Santo state (this study), Rio de Janeiro state (Rios 1994; this study).

Remarks: *Pseudoscilla babylonica* (Figure 3D–E) has been reported from Brazil and other regions in the western Atlantic as *Cingulina babylonica* (Warmke & Abbott 1962; Rios 1985, 1994; Abbott 1974; Vokes & Vokes 1983; Jong & Coomans 1988; Mello 1990) or *Odostomia babylonica* (Wise 1996; Redfern 2001). Odé (1993) stated that the genus *Cingulina* is normally and wrongly used for species from the western Atlantic, and

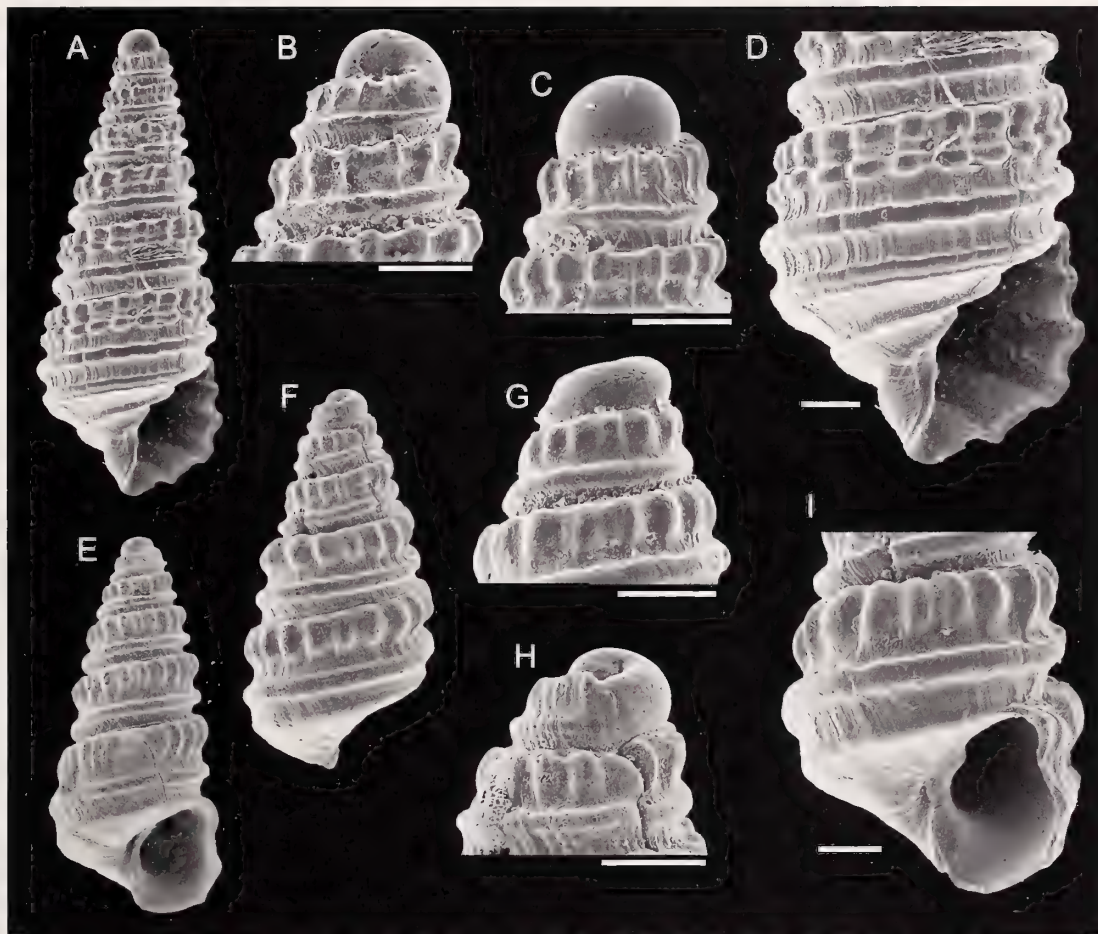


Figure 4. A–D. *Triptychus niveus* Mörch, 1875 (IBUFRJ 14080): A, whole shell (length: 2.7 mm); B–C, protoconchs; D, last whorl; E–I. *Triptychus litosbathron* n.sp.: E, holotype (MZSP 77065); F–G, paratype (MZSP 77066); H–I, paratype (IBUFRJ 12878); E–F, whole shells (respective lengths: 2.4 mm; 1.6 mm); G–H, protoconchs; I, last whorl. Scale bars: 200 µm.

introduced the combination *Pseudoscilla babylonia*, establishing that *Pseudoscilla* is not related to *Cingulina*. According to Odé (1993), *Pseudoscilla* is characterized by small, regularly conical shells, with sculpture consisting of strongly developed spiral cords, sometimes dissolved into separate knobs; *Cingulina*, on the other hand has more elongate shells, less strongly ornamented, and is restricted to the Pacific Ocean (Odé 1993).

Aartsen *et al.* (1998) reported *Pseudoscilla babylonia* from the North Atlantic Ocean. However, Peñas & Rolán (1999) reviewed the genus *Pseudoscilla* from West Africa, providing illustrations of the type-species (*Pseudoscilla miocaenica*), and concluded that the records of *P. babylonia* by Aartsen *et al.* (1998) were based on misidentifications of *Pseudoscilla bilirata* (Folin, 1870). According to Peñas & Rolán (1999), *Pseudoscilla babylonia* is restricted to the Western Atlantic.

Subfamily Pyramidellinae Gray, 1840

Genus *Triptychus* Mörch, 1875

Triptychus Mörch, 1875: 158. Type species: *Triptychus niveus* Mörch, 1875, by monotypy, St. Thomas.

Triptychus niveus Mörch, 1875

(Figure 4A–D)

Obeliscus (Triptychus) niveus Mörch (1875: 159).

Triptychus niveus: Abbott (1974: 300, fig. 3653); Warmke & Abbott (1962: 147, pl. 28e); Vokes & Vokes (1983: 32, pl. 30, fig. 17); Jong & Coomans (1988: 120, pl. 19, fig. 636); Diaz & Puyana (1994: 236, pl. LXIX, fig. 941); Redfern (2001: 145, pl. 65, fig. 603).

Triptychus niveus: Rehder (1943: 195, not illustrated)

Pyramidella vineta Dall, 1884: Synonymized by Abbott (1974).

Type locality: St. Thomas, Vieques, St. Martin.

Material examined: West Indies: IBUFRJ 14080, off Bonaire (12 m), 30.i.1998, [2]; IBUFRJ 14083, off Bonaire (4 m), 14.ii.1998, [1]; IBUFRJ 14084, off Bonaire (10 m), 30.i.1998, [1]; –Brazil: –Rio de Janeiro state: IBUFRJ 14078, Arquipélago de Santana, Macaé, v.1983, AG coll., [1]; IBUFRJ 14079, Bacia de Campos sta 22, [1].

Distribution: USA: Florida to West Indies (Abbott 1974; Warmke & Abbott 1962); Mexico: Yucatan Peninsula (Vokes & Vokes 1983); Caribbean: St. Thomas (Mörch 1875), Bahamas (Redfern 2001), West Indies (Rehder 1943; Jong & Coomans 1988), Colombia (Diaz & Puyana 1994); Brazil: Rio de Janeiro (this study).

Triptychus litosbathron n.sp.

(Figure 4E–I)

Type material: Holotype MZSP 77065, off Paraná state, PADCT 6577 (25°15.76'S / 45°04.62'W, 124 m). Paratypes: –Espírito Santo state: IBUFRJ 14081, off Espírito Santo state, REVIZEE sta vv24 (20°S / 34°54'W, 45 m), 27.ii.1996, NOAN coll., [1]; MNHN, off Espírito Santo state, REVIZEE sta vv24 (20°S / 34°54'W, 45 m), 27.ii.1996, NOAN coll. [1]; IBUFRJ 12878, off Espírito Santo state, REVIZEE sta D1 (20°48'S / 41°09'33"W, 69 m), 23.ii.1996, NOAN coll., [1]; MNRJ 10694, off Espírito Santo state, REVIZEE sta D1 (20°48'S / 41°09'33"W, 69 m), 23.ii.1996, NOAN coll., [1]; –São Paulo state: MZSP 86686, REVIZEE sta 6677 (24°40.75'S / 44°50.82'W, 137 m), [1]; MZSP 86688, REVIZEE 6662 (24°00.95'S / 43°55.54'W, 135 m), [5]; MZSP 86691, REVIZEE 6666 (24°17.13'S, 44°12.15'W, 163 m), [1]; MNHN, PADCT 6573 (24°42.608'S / 44°43.419'W, 155 m), [1]; –Paraná state: MZSP 77066, type locality, [1]; MNRJ 10941, type locality, [5]; –Santa Catarina state: MZSP 86693, PADCT sta 6641 (26°15'S / 45°53'W, 130 m) [1]; MZSP 86694, REVIZEE 6695 (26°17.134'S, 46°41.788'W, 153 m), [1]; MZSP 86695, PADCT 6606 (27°48.07'S / 47°24.04'W, 175 m), [1].

Type locality: 25°15.76'S / 45°04.62'W, 124 m; off Paraná state, Brazil.

Distribution: Only known from Brazil southeast-south coast: Espírito Santo state, São Paulo state, Paraná state.

Etymology: From the Greek *litos*: plain, simple; *-bathron*: base, pedestal. In allusion to the simple, unornamented base of this species.

Diagnosis: Small *Triptychus* species with smooth base, immersed protoconch and small chink-like umbilicus.

Description: Shell conic, holotype 2.4 mm in length. Teleconch with up to 5.5 whorls with sinuous outline, due to projections of whorl ornamentation. Suture deep. Protoconch heterostrophic with about 1.5 smooth whorls, with nucleus immersed in first teleconch whorl, forming an angle of about 180° with teleconch main axis; diameter about 250 µm. Two deep and wide, channeled spiral furrows, bearing microscopic axial growth lines, one just above the suture, the other in the midline of each teleconch whorl; between the two furrows, there is a strong, wide, smooth spiral cord; another, stronger spiral cord, just below the suture, is formed by a spiral row of about 18 rounded nodules, axially elongated. Base slightly concave, with microscopic axial ribs and with its adapical periphery marked by a peripheral smooth spiral cord; with a very small chink-like umbilicus, sometimes partially covered. Aperture rhomboid, with a columellar fold medium to weakly projected. Outer lip thin and nearly straight.

Remarks: *Triptychus niveus* has a wide geographic range in the western Atlantic, including localities in the U.S.A. and Caribbean (see distribution for references) and the records of this paper from Brazil (Figure 4A–D), where it has been collected on the southeast coast (about 23°S); *Triptychus litosbathron*, on the other hand, is restricted to localities on the southeastern and south coasts of Brazil (about 20°–25° S).

The inclusion of *Triptychus litosbathron* (Figure 4E–I) in this genus is somewhat doubtful. The shell has the same general shape, a somewhat more immersed protoconch and similar sculpture, with two spiral cords on each teleconch whorl, the abapical one is nodulose, the adapical smooth (Figure 4E–F, I); in *T. niveus*, there are one smooth adapical spiral cord and two nodulose abapical spiral cords on each teleconch whorl (Figure 4A, D); however, this pattern is not present on the first three adult whorls, which have only one nodulose spiral and the smooth one (Figure 4A–B). In addition, *T. litosbathron* has an almost smooth base (Figure 4I), lacking the spiral cords present in *T. niveus* (Figure 4D). In spite of all these differences, this seems to be the best generic allocation for the new species herein described, considering also, that it is not desirable to introduce a new generic name in the already confused Pyramidellidae.

Diaz & Puyana (1994: pl. LXIX, fig. 936) illustrated a shell named *Odostomia (Miralda)* sp. The shell is very similar to *Triptychus litosbathron*, but has an additional spiral cord on the base.

Genus *Peristichia* Dall, 1889

Peristichia Dall, 1889: 339. Type species: *Peristichia toreta* Dall, 1889, Florida Keys (USA), by original designation.

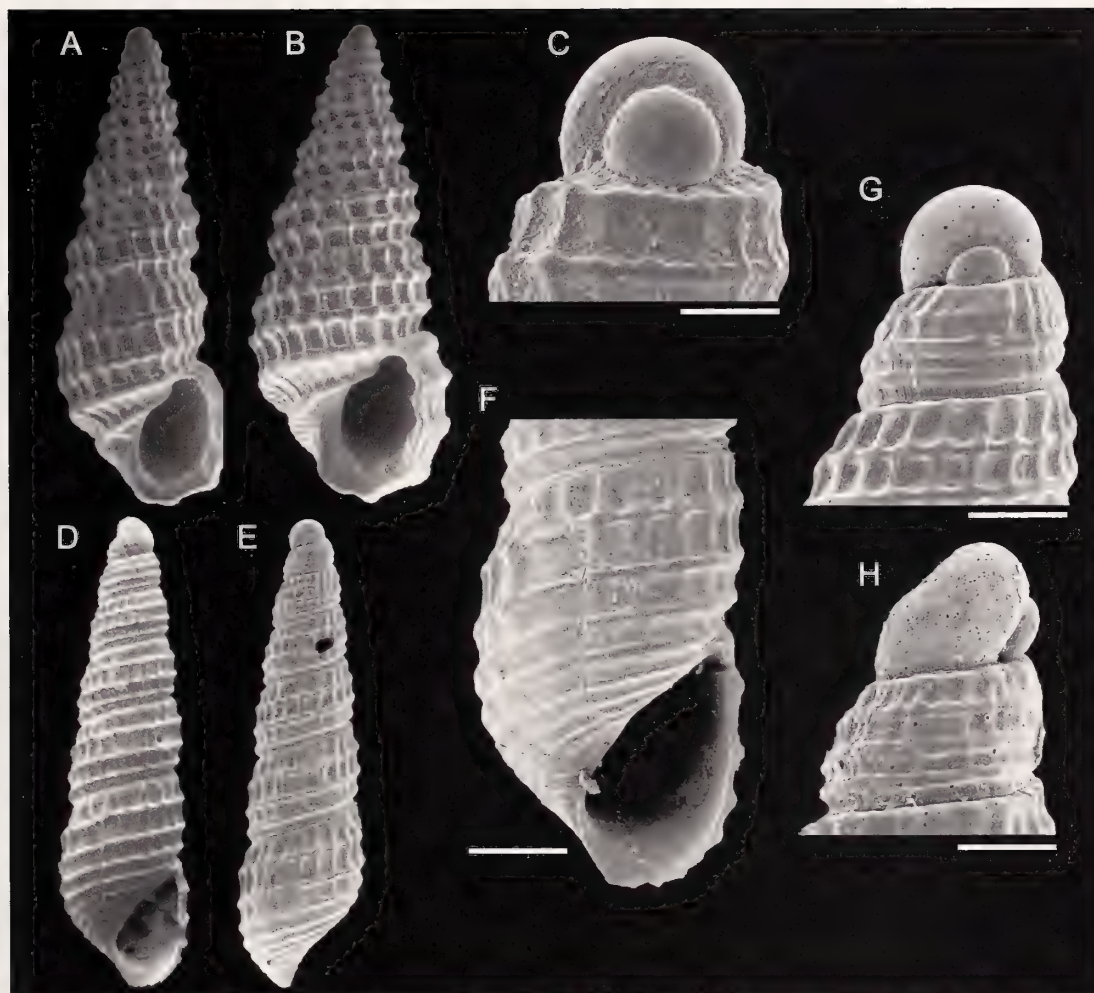


Figure 5. A–C. *Peristichia agria* Dall, 1889. A, MNHN; B, MNRJ 10824; C, IBUFRJ 7774; A–B, whole shells (respective lengths: A, 4.0 mm; B, 4.1 mm); C, protoconch; D–H, *Peristichia lepta* n.sp.: D–G, holotype (MZSP 77062); H, aperture (MZSP 77063). D–E, whole shell (length: 4.2 mm); F, last whorl; G–H, protoconchs. Scale bars: 200 μ m.

Peristichia agria Dall, 1889

(Figure 5A–C)

Peristichia agria Dall, 1889: 340. Rehder (1943: 195, pl. 20, fig. 4); Abbott (1974: 300, fig. 3655); Diaz & Puyana (1994: 236, pl. LXIX, fig. 942); Vokes & Vokes (1983: 32, pl. 30, fig. 18); Rios (1985: 165, pl. 54, fig. 786, 1994: 188, pl. 62, fig. 879); Mello & Perrier (1986: 139, not illustrated; Mello (1990: 41, fig. 11); Barros (1994a: 74, not illustrated).

Type locality: off Cape Hatteras, 63 fms.

Material examined: Bahia state: MNHN, Paulista (praia da Conceição), [2]; MNRJ 10824, Itaparica (praia do Despacho), [3]; MNHN, environs de Recife, [2]; MNHN, Cabo (praia de Gaibu), [2]; MNHN,

Itamaracá (praia de Jaguaribe), [4]; MNHN, Cabo (pedras pretas), [3]; MNHN, Paulista (Maria Farinha), [6]; MNHN, São Luiz (areia preta), [1]; MNHN, Paulista (Maria Farinha), [1]; MNHN, Cabo (praia de Gaibu), [1]; –Rio de Janeiro state: Col.Mol.UERJ 3338, Ilha Grande sta 15 (Ponta Grande Timuiba, 23°3.762'S 44°36.038'W, 7 m), [5]; Col.Mol.UERJ 3337, Ilha Grande sta 16 (Rochedo São Pedro, 23°2.868'S 44°32.722'W, 10 m), [1]; IBUFRJ 13686, Angra dos Reis (praia da Figueira), 1998, [1]; IBUFRJ 7774, GEOMAR XII sta 46 (21°30'S, 40°54.8'W, 27 m), viii.1979, [1]; IBUFRJ 2559, Prainha, Arraial do Cabo, [3].

Distribution: USA: North Carolina to Florida (Dall 1889; Abbott 1974); Mexico: Yucatan Peninsula (Vokes & Vokes 1983); Caribbean: Colombia (Diaz & Puyana 1994); West Indies (Rehder 1943); Brazil:

Ceará to Santa Catarina (Mello 1990; Rios 1994; Barros 1994a).

Peristichia lepta n.sp.

(Figure 5D–H)

Peristichia agria: Farinati (1993: 306, fig. 16).

Type material: Holotype MZSP 77062. Paratypes: MZSP 77063, off São Paulo state, PADCT sta. 6579 (24°42.302'S, 45°18.831'W, 84 m), [16]; MZSP 77064, off São Paulo state, REVIZEE sta 6669 (24°7.42'S, 44°42.22'W, 101 m), [2]; IBUFRJ 9015, Camburi, Espírito Santo state, Eq. Zoo Coll., 15.xii.1987, [2]; IBUFRJ 14085, GEOMAR XII sta 108, 29.viii.1979 NOAS coll., [1]; MNRJ 10693, Ilha Grande sta 36 (Ponta Alta de Parnaioaca, 23°12.25'S, 44°30.35'W, 35 m), Rio de Janeiro state, [2]; Col.Mol.UERJ 3335, Ilha Grande sta 36 (Ponta Alta de Parnaioaca, 23°12.25'S, 44°30.35'W, 35 m), Rio de Janeiro state, [3]; MNHN, Ilha Grande sta 36 (Ponta Alta de Parnaioaca, 23°12.25'S, 44°30.35'W, 35 m), Rio de Janeiro state, [2].

Type locality: off Paraná state, Brazil; REVIZEE sta 6656 (25°22.1'S, 46°47.5'W, 70 m).

Distribution: Only known from southeast-south coasts of Brazil: Espírito Santo, Rio de Janeiro, São Paulo and Paraná states; and an additional record from Baía Blanca, Argentina (Farinati 1993).

Etymology: From the Latin *leptos*: fine, small, thin, delicate. An allusion to the slender shell of this species.

Diagnosis: *Peristichia* species with slender shell of almost straight whorled outline and base with four smooth spiral cords of equal strength.

Description: Shell white, elongate, slender and conical, with about six whorls of almost flat-sided outline; holotype 4.2 mm in length; imperforate. Suture somewhat deep. Protoconch heterostrophic helicoid, with about two whorls forming an angle of about 110° to the shell main axis, diameter about 325 µm. Axial ribs orthocone, or slightly opisthocline, slender, with upper summits forming small nodules projecting slightly over adapical suture; 22 on body whorl of holotype; interspaces as wide as the ribs, bearing microscopic axial growth lines. Spiral sculpture formed by three narrow cords crossing the axial ribs, forming small rising nodules, well visible on the outline of the whorls, giving rise to a cancellate pattern; median spiral cord stronger than the other two; lower cord forming a channeled furrow below it and above suture. Base somewhat elongate, with about four or five smooth, equally strong spiral cords. Aperture somewhat pyri-

form, pointed adapically. Outer lip thin. Columellar fold absent.

Remarks: Rehder (1943) discussed the affinities of *Peristichia*, considering it as a full genus, close to *Triptychus*. *Peristichia lepta* (Figure 5D–H) has some similarities to other species from the western Atlantic included in *Peristichia*, such as *Peristichia agria* (Figure 5A–C) and the type-species *Peristichia toreta* Dall, 1889 (illustration of specimen by Perry & Schwengel 1955: pl. 23, fig. 160), mainly in the general elongate shell shape, sculpture pattern and protoconch; but differs in the absence of a columellar fold and, mainly, by the approximately four spiral cords on the base, whereas the other species of *Peristichia* have only one.

The most similar species to *Peristichia lepta* is *Peristichia agria*, which it resembles in the sculpture pattern, formed by thin, almost orthocone axial ribs crossed by thin spiral cords, giving rise to squared interspaces and small rounded nodules (Figure 5A–B). In *Peristichia lepta*, however, the sculpture is consistently weaker, and the shell is more cylindrical and the whorls less convex in outline (Figure 5D–F); whereas in *P. agria*, the last whorl is somewhat globose, with strongly convex outlines (Figure 5A). Also, in *Peristichia lepta*, there are more numerous and weaker spiral cords on the base (Figure 5F); whereas *P. agria* has a single, stronger spiral cord in the middle of the base (Figure 5A–B).

Peristichia agria has a wide distribution in the western Atlantic, from U.S.A. to southern Brazil (see references in distribution). The known distribution of *Peristichia lepta* is southeast-south coasts of Brazil. Farinati (1993, 1993: 306, fig. 16) illustrated a specimen of *Peristichia lepta*, from the Holocene of Bahía Blanca, Argentina, with the name *P. agria*. This record from Argentina enlarges the geographical and geological distribution of this new species.

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Galba truncatula Müller, 1774 (Pulmonata: Lymnaeidae) in Argentina: Presence and Natural Infection by *Fasciola hepatica* (Linnaeus, 1758) (Trematoda: Digenea)

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Abstract. We report the finding of *Galba truncatula* in Argentina. In June and August 2006, 157 snails were collected from a stream in Sierras del Palauco, Province of Mendoza, northern Patagonia, Argentina. *Fasciola hepatica* infection was detected in one of 50 specimens collected in June. In the Americas, this snail was reported from Bolivia and Chile, and its occurrence in Argentina may reflect an ongoing process of geographic expansion. In Argentine Patagonia, *Lymnaea viatrix* has been regarded as the only lymnaeid involved in the transmission of *F. hepatica*, but our results suggest that *G. truncatula* may also be playing a role.

INTRODUCTION

Mollusks are used as first intermediate hosts by all species of digenetic trematodes (Esch et al., 2002). In particular, the cosmopolitan snails of the family Lymnaeidae are involved in the transmission of some digeneans of veterinary and medical importance, such as *Fasciola hepatica* (Linnaeus, 1758), the causative agent of fasciolosis (Malek, 1985).

The endemicity of fasciolosis in a region depends on the presence of intermediate hosts adapted to particular environmental conditions, and therefore the identification of local lymnaeid species is essential for the design of effective control strategies. In the native fauna of Argentina, species of Lymnaeidae so far reported are *Lymnaea diaphana* King, 1830; *Lymnaea pictonica* Rochebrune & Mabilie, 1885; *Lymnaea viatrix* Orbigny, 1835 (Hubendick, 1951; Paraense, 1976, 1982; Malek, 1985; Kleiman et al., 2004); and *Pseudosuccinea columella* Say, 1817 (Paraense, 1982; Prepelitchi et al., 2003). At present, the only species incriminated in the transmission of *F. hepatica* are *P. columella* (Prepelitchi et al., 2003) and *L. viatrix*, which shows the broadest distribution (Rubel et al., 2005; Cucher et al., 2006; Kleiman et al., 2007).

In this work, we report *Galba truncatula* Müller, 1774 in Argentina, and provide evidence of natural infection of this snail with *F. hepatica*.

MATERIAL AND METHODS

The study was performed in a stream at an altitude of 1943 m, located in Sierras del Palauco (35°57'S 69°24'W), Department of Malargüe, Province of Mendoza, northern Patagonia, Argentina (Figure 1). The climate in the study area is cold and arid, with a mean annual temperature of 21.3°C (mean temperature of the coldest month, July: –2.3°C; mean temperature of the warmest month, January: 27.9°C). Winter is the rainy season, and the mean annual precipitation is 198 mm. Biogeographically, the region is included within the Andean–Patagonian domain, Patagonian province, Payunia district, which is characterized by xerophytic vegetation (Cabrera & Willink, 1980). The human population is small and houses are scattered over a large area (density: <1 inhabitant per km²). The economic activity is mainly based on the rearing of goats, followed by sheep and cattle. Local inhabitants have mentioned the presence of *F. hepatica* in their livestock.

Two surveys were performed, one in June and one in August 2006 (winter). In the studied stream, 157 snails were hand-collected between 12:00 pm and 4:00 pm. Water temperature and pH were recorded simultaneously. Samples of aquatic vegetation associated with the snails were taken for further identification. Snails were transported alive to the laboratory in plastic flasks



Figure 1. Map of Argentina (sparse dots). The asterisk indicates the studied area, Sierras del Palauco, in the Province of Mendoza (dense dots).

containing water and vegetation from the collecting site.

The taxonomic determination of snails was performed in 33 of the largest specimens collected from both surveys, so as to increase the probability of sexual

maturity. These were relaxed, sacrificed, preserved in Railliet-Henry's fluid (Paraense, 1984), and taxonomically determined by features of the shell and the male reproductive system. Shell measures recorded from these specimens were as follows: length from the apex to the anterior margin (shell length, SL); maximum shell width (SW); aperture length (AL); and aperture width (AW). The following ratios were calculated: SL/SW, SL/AL, and penis sheath length/prepuce length. The shell length was measured in the 124 remaining snails. All measurements were made using a stereoscopic microscope with a graduated eyepiece.

Live snails were individually placed in small containers with dechlorinated tap water and then exposed to light to stimulate cercariae shedding. Preserved and live snails were dissected to detect trematode larvae in viscera. Determination of *F. hepatica* infection was based on the morphological features of mature cercariae and adults recovered from experimentally infected Wistar rats.

RESULTS

The stream was a shallow and permanent water body with moderately fast-flowing water and rocky bottom. Water temperature was 9.8 and 8°C, and pH varied from 5 to 6 in the first and second surveys, respectively. Snails were found attached to the underside of submerged stones and to aquatic vegetation composed of species of the Haloragaceae and Amaranthaceae.

Snails were identified as *G. truncatula* by comparisons with European specimens of confirmed identity and with illustrations previously published (Yahia, 1997; Samadi et al., 2000; Glöer, 2002). In addition, they were distinguished from lymnaeid species previously reported in Argentina (Table 1). Snails that were not used for taxonomic determination ($n = 124$) were

Table 1

Main morphological characters used to differentiate *Galba truncatula* from other lymnaeid species so far reported from Argentina. nd: no data available.

	<i>G. truncatula</i>	<i>L. viatrix</i>	<i>L. diaphana</i>	<i>L. columella</i>	<i>L. pictonica</i>
shell	less developed body whorl, with rounded shoulder; long spire			voluminous body whorl, with vaulted shoulder; short spire	
prostate	stomach-shaped, increases in diameter toward vas deferens	ovoid or pear-shaped	voluminous, irregular	thread-like or ribbon-like	nd
penial sheath/prepuce ratio	1/4 to 1/5	1/1 to 1/3	1/1 to 1/2	1/6 to 1/8	nd
relative size of penial complex	++	+++	++++	+	nd
sources	Hubendick (1951) Godan (1979) Glöer (2002) Rondelaud (2007) present study	Paraense (1976) material collected by us	Paraense (1984) material collected by us	Paraense (1983) material collected by us	Hubendick (1951)

Table 2

Shell morphometrics (mean, standard deviation and min-max) of *Galba truncatula* from Sierras del Palauco, Province of Mendoza, Argentina. Measurements were made in 33 specimens.

	mean \pm SD (mm)	min-max (mm)
Shell length	8.00 \pm 0.78	6.00–9.50
Shell width	4.01 \pm 0.39	3.16–4.90
Aperture length	3.90 \pm 0.38	2.84–4.74
Aperture width	2.16 \pm 0.27	1.42–2.69
Shell length/Shell width	2.00 \pm 0.10	1.71–2.22
Shell length/Aperture width	2.05 \pm 0.12	1.79–2.43

assumed to belong to *G. truncatula* because they were identical in external appearance to those already identified.

The length of all collected snails ranged between 1.74 and 10.27 mm. Shell measures obtained from 33 of the largest specimens are shown in Table 2. In the latter group, the penis sheath length to prepuce length ratio was 1:4 to 1:5. The shell and the most conspicuous organs of the male genitalia are shown in Figure 2 A–C.

Voucher specimens were deposited in the National Collection of Invertebrates at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN-In, voucher number 37107).

Snail infection with *F. hepatica* was detected in the survey of June, with a prevalence of 2% (1/50). The infected snail measured 5.06 mm in shell length.

DISCUSSION

According to Heppleston (1972), *G. truncatula* reaches sexual maturity at a shell length of about 4.5 mm. On

this basis, all snails used for species identification and the one infected with *F. hepatica* were adults. In the Old World, *G. truncatula* is the most important intermediate host of *F. hepatica* in Europe and some parts of Asia and Africa (Jabbour-Zahab et al., 1997). This snail is found in freshwater environments located at different altitudes, from lowlands at sea level to plateaus and mountain areas above 2000 m asl (Goumghar et al., 2001; Vignoles et al., 2002). It can colonize artificial and natural, permanent and temporary freshwater habitats (Heppleston, 1972; Hammami & Ayadi, 1999). This is probably accounted for by a remarkable ability to adapt to a wide range of water conditions including salinity and pH (Hammami & Ayadi, 1999). In addition, *G. truncatula* is able to withstand temperature and humidity fluctuations (Heppleston, 1972), drought through aestivation (Torgerson & Claxton, 1999), and very low temperatures through hibernation (Vareille-Morel et al., 1998). In Sierra del Palauco, snails were active at water temperatures of 8–9.8°C, in agreement with Heppleston (1972) who suggested a threshold value of 6°C.

In the Americas, the presence of *G. truncatula* has been ascertained in the Bolivian Altiplano by anatomical (Oviedo et al., 1995) and isoenzymatic studies (Jabbour-Zahab et al., 1997), as well as by 18S rDNA sequence analysis (Bargues et al., 1997). The results of these studies led authors to hypothesize that this species was introduced from Europe to Bolivia. Thus, the high ecological plasticity of *G. truncatula* may have enabled it to colonize successfully habitats under extreme conditions of very high altitude, between 3500 and 4200 m above sea level (asl) (Mas-Coma et al., 1999). This species has also been found in Valdivia, Chile (Yahia, 1997), a site located closer (39°48'00"S 73°13'59"W) to Sierra del Palauco, but with different

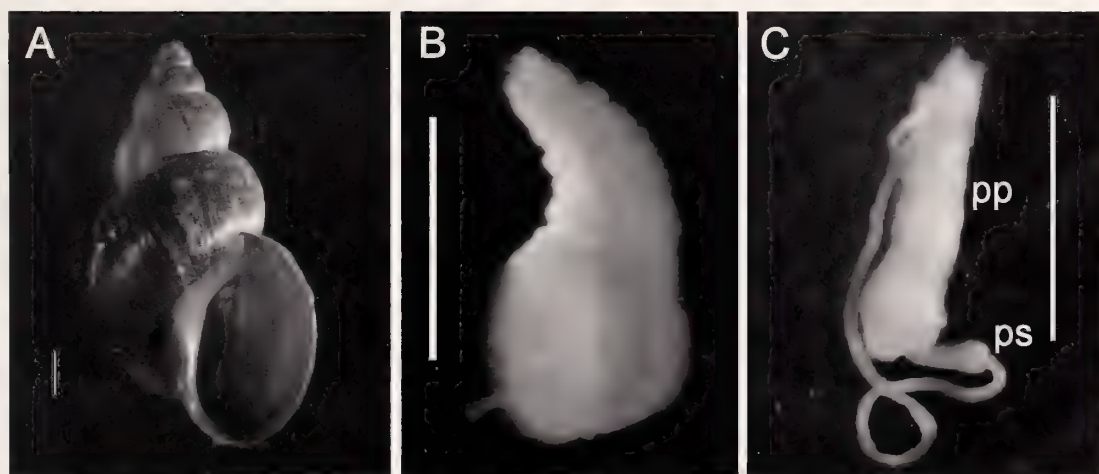


Figure 2. *Galba truncatula* from Sierras del Palauco, Province of Mendoza, Argentina. A: ventral view of shell; B: prostete; C: penial complex showing prepuce (pp) and penial sheath (ps). Scale bar = 1 mm.

environmental conditions (e.g., 5 m asl, temperate-rainy climate).

Although in Europe *G. truncatula* has been characterized as a mud, amphibious snail (Heppleston, 1972; Torgerson & Claxton, 1999), in Sierra del Palauco it was found attached to the underside of submerged stones. This fact suggests "a more aquatic" behavior, in accordance with that observed in snails of the northern Bolivian Altiplano (Mas-Coma, 1998).

In the endemic provinces of Argentine Patagonia, *L. viatrix* has been considered the only intermediate host involved in the transmission of *F. hepatica* (Kleiman et al., 2004, 2007; Rubel et al., 2005). However, the occurrence of infection in *G. truncatula* reported herein raises further questions regarding its importance in the local transmission cycle, because of the major role played by this species in Europe and the Bolivian Altiplano.

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Diel Patterns of Vertical Distribution in Euthecosomatous Pteropods of Hawaiian Waters

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Abstract. Nineteen species of euthecosomatous pteropods were identified from epipelagic waters off Hawaii. Diel patterns of vertical distribution, abundance, and shell size were assessed from 32 tows taken through five depth intervals to 300 m during day and night periods using opening-closing 70 cm Bongo nets. Six species (*Limacina trochiformis*, *Creseis* sp., *C. virgula conica*, *Diacria danae*, *Diacavolinia angulosa*, and *Diacria costata*) were epipelagic and showed limited to no diel differences. Thirteen species (*L. inflata*, *Styliola subula*, *L. bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa*, *L. lesueuri*, *C. inflexa*, *Cuvierina columnella*, *Hyalocylis striata*, *Diacria maculata*, *Cavolinia gibbosa*, and *Diacria major*) were either epipelagic/mesopelagic or mesopelagic, and showed an increase in total mean abundance at night. Diel differences in vertical distribution are most parsimoniously interpreted as upward nocturnal migrations. The results of this study are in general agreement with those obtained for the same species in the North Atlantic Ocean and Caribbean Sea.

INTRODUCTION

The euthecosomatous (or shelled) pteropods are widely distributed in the world's oceans and the majority of species dwell in the epipelagic zone, although a few are mesopelagic or bathypelagic (Bé and Gilmer, 1977). Our understanding of their vertical distribution patterns is based mainly on studies that have employed stratified-oblique or discrete-depth tows carried out in the North Atlantic Ocean (Wormelle, 1962; Myers, 1967; Haagensen, 1976; Wormuth, 1981; and Andersen et al., 1997). The most comprehensive of these studies (Wormuth, 1981) employed stratified tows taken through discrete depth intervals to 1000 m during day and night periods. *Limacina inflata* (d'Orbigny, 1836), *L. lesueuri* (d'Orbigny, 1836), *Styliola subula* (Quoy and Gaimard, 1827), and *Clio pyramidata* Linnaeus, 1767 were characterized as strong migrators, with peak abundances at depths of 200–400 m during the day and <100 m at night. *Limacina trochiformis* (d'Orbigny, 1836), *L. bulimoides* (d'Orbigny, 1836), *Clio cuspidata* (Bosc, 1802), *Creseis acicula* (Rang, 1828), and *C. virgula* (Rang, 1828) showed highest daytime and nighttime abundances at depths <100 m (i.e., they were shallow-water non-migrators).

Vertical distribution data in the Pacific Ocean come from only two studies. The first was conducted by McGowan (1960) in the North Pacific and sampled the

upper 140 m during day and night periods by oblique tows with continuously open and opening-closing nets. *Creseis virgula clava* (Tesch, 1948), *Clio pyramidata*, *Limacina inflata*, and *L. helicina* (Phipps, 1774) were captured in greater numbers at night than during the day, suggesting upward nocturnal migrations, while *Limacina trochiformis* and *Cavolinia longirostris* (de Blainville, 1821) were collected in comparable numbers during the day and at night. Twenty other species were identified, but no vertical distribution data were given. In the second study (Tanaka, 1970), vertical distribution records for individual species were not given except for *Limacina inflata*, which had maximal numbers at 50 m at night (but ranged downward to 550 m) and had an even distribution between the surface and 400 m during the day.

The present study on the diel vertical distribution and abundance of euthecosomes is the first from the Pacific Ocean based on replicated, opening-closing net samples. Oblique tows were taken through five depth intervals in the upper 300 m of the water column during day and night periods, and vertical patterns of distribution, density, and shell size are characterized for 19 species.

MATERIALS AND METHODS

The plankton samples used here come from a previous study designed to determine diel patterns of vertical distribution and abundance of squid paralarvae (Young and Harman, 1985 and Harman and Young, 1985) and heteropod gastropods (Seapy, 1990). Plankton tows were taken in waters southwest of the

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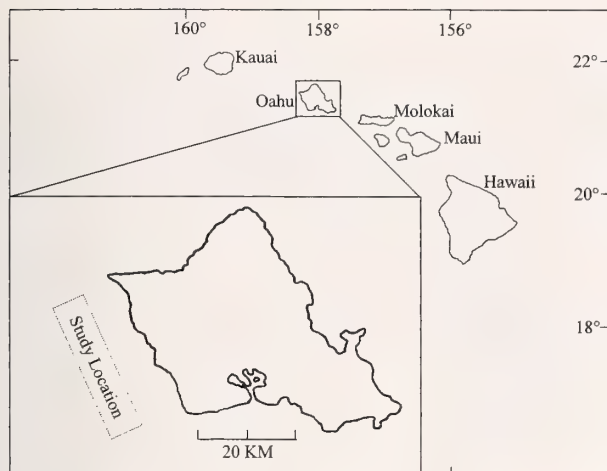


Figure 1. Hawaiian Archipelago and the location of the sampling area off the southwest side of the island of Oahu.

Hawaiian island of Oahu (Figure 1) aboard the R/V *KANA KEOKI* of the University of Hawaii between 9 and 15 April 1984. The study area was located in waters that averaged 2000 m in depth and ranged from 11 to 20 km off shore (Figure 1). Samples were collected with opening-closing, 70-cm diameter (0.385 m²) Bongo nets constructed of 0.5 mm Nytex cloth. The nets were fished obliquely through six target depth intervals (0–50, 50–100, 100–150, 150–200, 200–300 and 300–400 m) comprising the epipelagic zone off Hawaii (Young et al., 1980) for thirty minutes in each depth stratum during day and night periods (Figure 2). Unfortunately, difficulties encountered in completing tows in the 300–400 m interval resulted in only one successful tow during the day between 280 and 380 m (Seapy, 1990). Because there was no replication and no nighttime samples, the 300–400 m interval was omitted from the present study.

Previous research (Snider, 1975; cited in Wormuth, 1986) has shown that collection of larvae and young post-metamorphic individuals of *Limacina inflata* and *L. trochiformis* was greatly increased by using nets with a mesh size of 0.183 mm instead of 0.505 mm. Shell diameter at metamorphosis of *L. inflata* and *L. retroversa* (Flemming, 1823) is about 0.4 mm (discussed in Lalli and Gilmer, 1989). Since this study does not include larvae, those post-metamorphic individuals of limacinids between 0.4 and 0.5 mm were undoubtedly undersampled. Based on Snider's (1975) size-frequency plots (reproduced in Wormuth, 1986), a 0.505 mm net collects about half as many individuals in the size range of 0.4–0.5 mm as a 0.183 mm net.

A Benthos Time-Depth Recorder was attached to the Bongo net frame, and the starting and finishing depths for each depth stratum were determined subsequent to the tows from resultant time-depth plots.

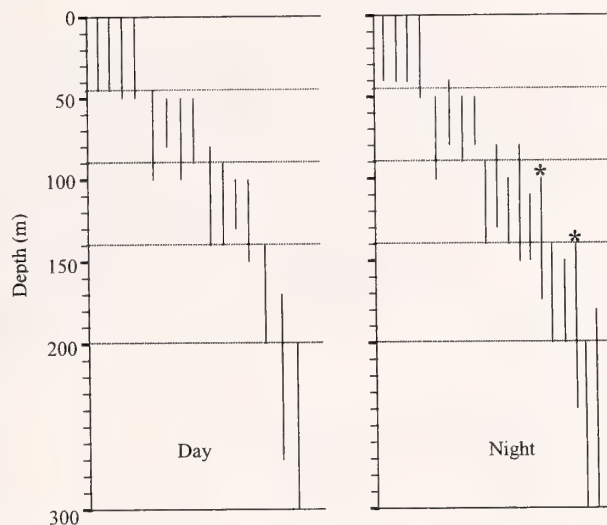


Figure 2. Depth ranges of tows taken during day and night periods. Vertical lines represent depth ranges of individual tows. Horizontal dotted lines indicate the adjusted depths of each sample depth interval. Asterisks mark the two tows that were not used in the analysis.

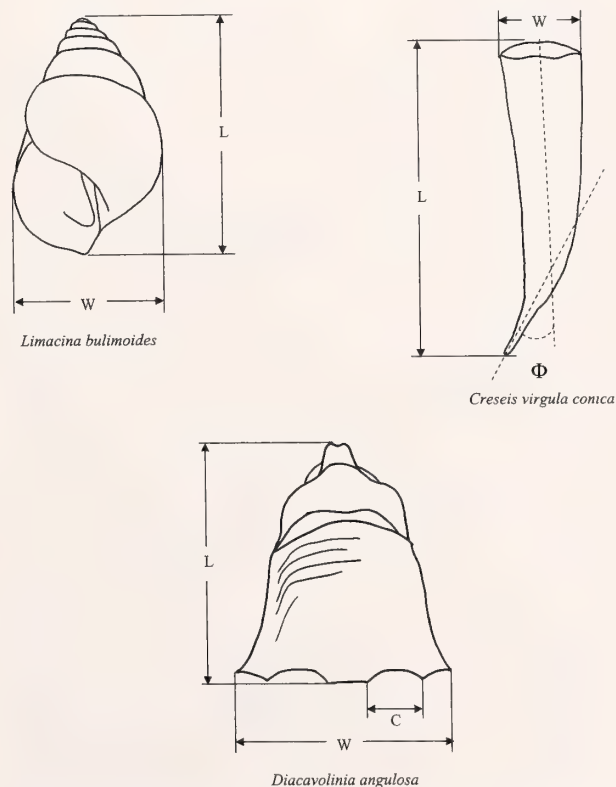


Figure 3. Euthecosome shell morphometrics. Where: L = length, W = width, Φ = posterior angle, and C = caudal fold width.

Table 1

Water column densities (numbers of individuals beneath 100 m² of ocean surface) for day and night periods and assignment of species to vertical groupings. To facilitate comparisons between species, the nighttime densities are also expressed as percentages. Differences in water column densities between day and night periods were assessed using a χ^2 test (where: s = significant at $P = \leq 0.05$ and ns = not significant). Each species was placed into either an epipelagic (=1) or epipelagic/mesopelagic and mesopelagic (=2) group (see results). Vertical groups shown in parentheses are hypothesized due to lack of statistical support.

Species	Density			Significance	Vertical group
	Night	Percentage	Day		
<i>Limacina inflata</i>	1514.9	34.5	93.2	s	2
<i>Styliola subula</i>	734.6	16.7	56.0	s	2
<i>Limacina trochiformis</i>	733.6	16.7	1014.4	s	1
<i>Limacina bulimoides</i>	409.2	9.3	209.1	s	2
<i>Creseis acicula</i>	233.6	5.3	57.7	s	2
<i>Clio pyramidata</i>	201.8	4.6	14.8	s	2
<i>Cavolinia globulosa</i>	180.4	4.1	142.5	s	2
<i>Limacina lesueurii</i>	153.4	3.5	3.9	s	2
<i>Creseis</i> sp.	63.3	1.4	57.5	ns	1
<i>Cavolinia inflexa</i>	46.6	1.1	23.0	s	2
<i>Creseis virgula conica</i>	45.1	1.0	57.6	ns	1
<i>Diacria danae</i>	18.9	0.4	21.5	ns	1
<i>Cuvierina columnella</i>	17.9	0.4	0.0		(2)
<i>Diacavolinia angulosa</i>	10.9	0.3	17.4	ns	1
<i>Diacria costata</i>	10.0	0.2	7.9	ns	1
<i>Hyalocylis striata</i>	7.7	0.2	0.0		(2)
<i>Diacria maculata</i>	3.5	0.1	0.0		(2)
<i>Cavolinia gibbosa</i>	2.0	0.1	0.0		(2)
<i>Diacria major</i>	0.5	<0.1	0.0		(2)
Total	4387.9		1776.5		

The dates and times of the tows used here are given in Nigro (2002). Recorded ranges for the depth strata were reasonably accurate in the 0–50 and 50–100 m targeted intervals, but progressively less so for the deeper intervals (Figure 2). The cause of the inaccuracies at increased depth was that prior to each tow, we had to estimate the length of wire paid based on the wire angle (determined using a hand-held wire angle indicator) and the maximal target depth (by division of the target depth (m) by the cosine of the wire angle). Because the cable is progressively less likely to remain straight as depth increases, achieving the target depths by this method become progressively less accurate.

Based on the recorded depth ranges of the tows, five sample depth intervals were established: 0–45, 45–90, 90–140, 140–200, and 200–300 m (Figure 2). These depth intervals were chosen to minimize the amount of overlap between adjacent intervals, as most tows ranged somewhat outside their targeted depth interval. Tows that ranged outside a depth interval but that fished mostly within it were considered to have fished entirely within that interval. Also, tows that ranged through only part of a depth interval but did not extend into another one were considered to have fished entirely within it. We made one exception to this requirement; the first of two daytime tows in the 200–300 m sample

depth interval was assigned to that interval, even though it ranged 30 m into the 140–200 m interval.

Two plankton samples (port and starboard) were collected during most tows. During five tows, however, the port or starboard net became fouled and only the sample from the open net was available. Also, either the port or starboard sample was not used from four tows because of poor sample preservation. Altogether, 55 plankton samples from the 32 tows were used in the analysis. At least four replicate samples each for the day and night periods were used from the first three depth intervals (0–45, 45–90, and 90–140 m). One and two samples for the day and night periods, respectively, were used for the 140–200 m depth interval. For the 200–300 m depth interval, two samples were used for each diel period.

The volume of water filtered during each tow was calculated based on the number of revolutions recorded by calibrated T.S.K. Model OI-210 Flow Meters mounted inside the frame of each net. The volume of water filtered during each tow averaged of 2841 m³ and ranged from 1142 to 6027 m³ (Nigro, 2002). Expendable Bathythermograph (XBT) casts were made daily during the cruise. There was little variability between the results from day to day. Briefly, the average surface temperature was about 25°C and the mixed layer

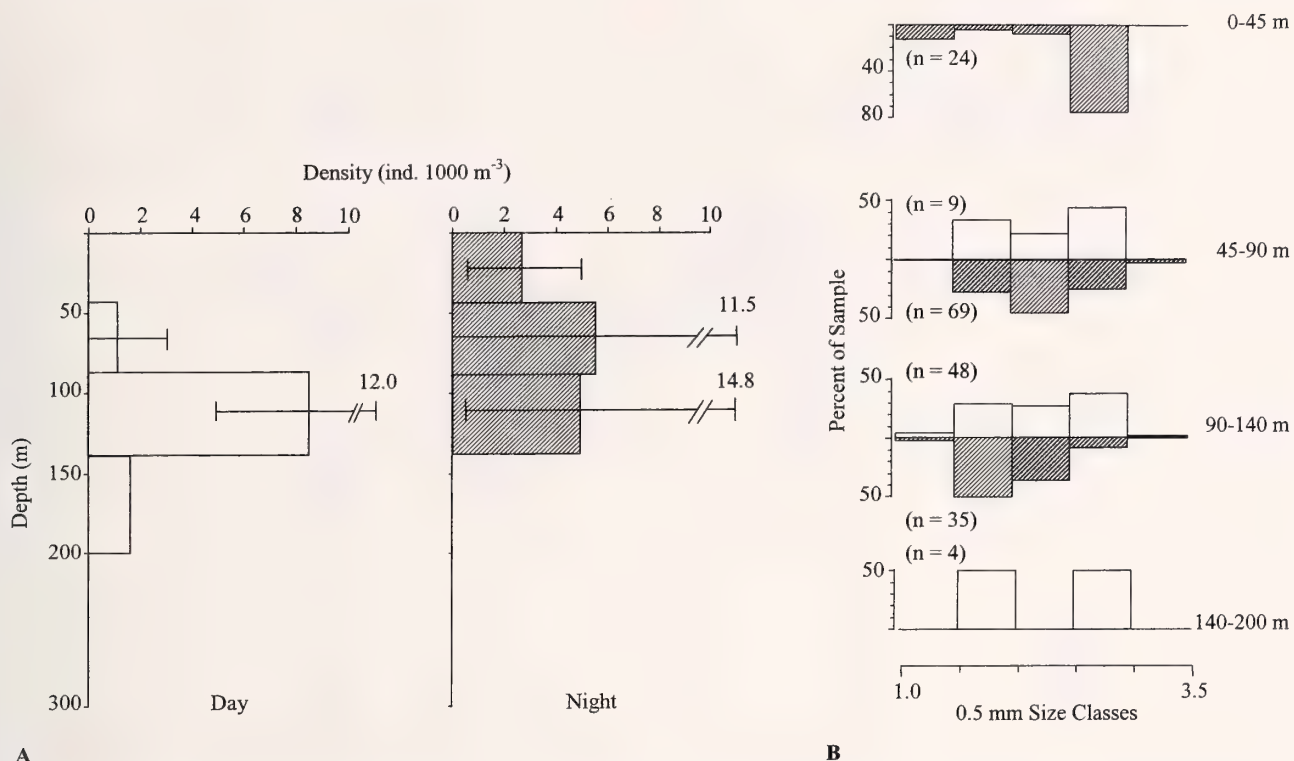


Figure 4. *Creseis* sp. (A) Mean densities (ind. 1000 m⁻³) in each depth interval during day (open bars) and night (hatched bars) periods. At the midpoint of each depth interval, ranges of densities among replicated tows are indicated by horizontal bars. (B) Percent of individuals in each size class from each depth interval during the day (open bars above the x-axis) and night (hatched bars below the x-axis). The number of specimens measured is indicated in parentheses.

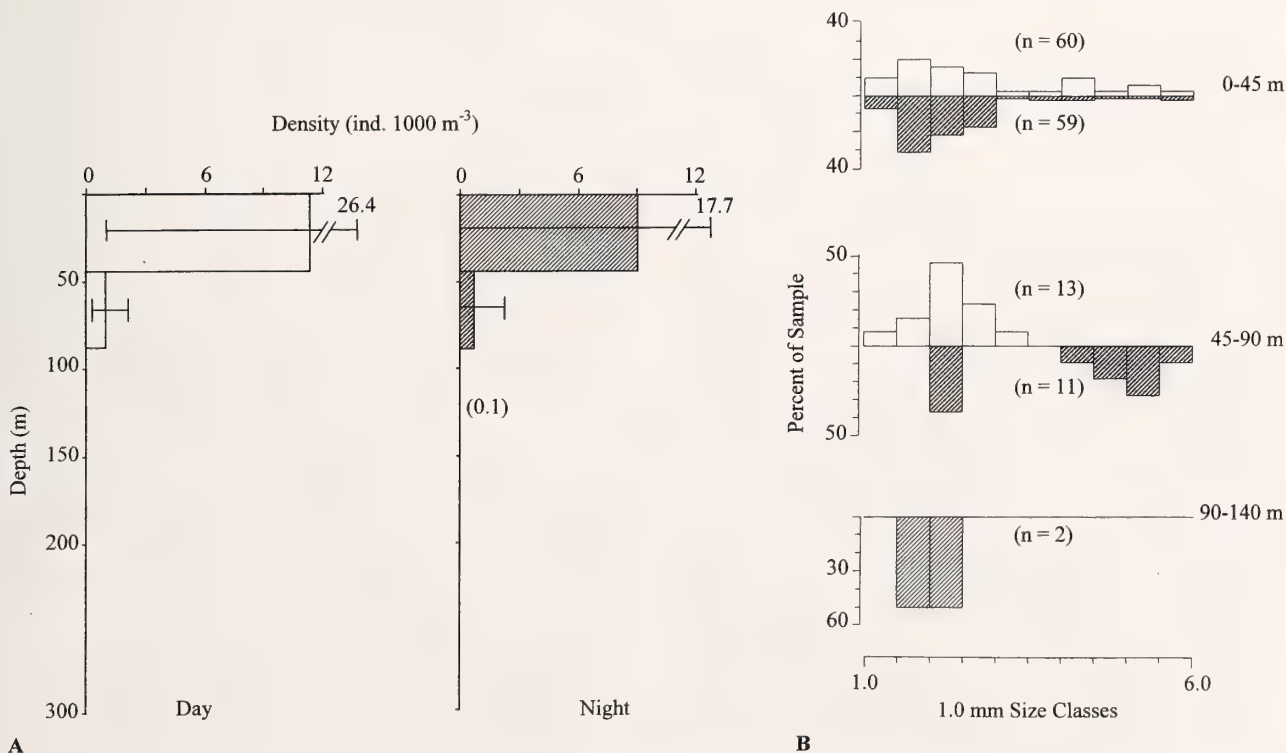


Figure 5. *Creseis virgula conica*. Legend as for Figure 4.

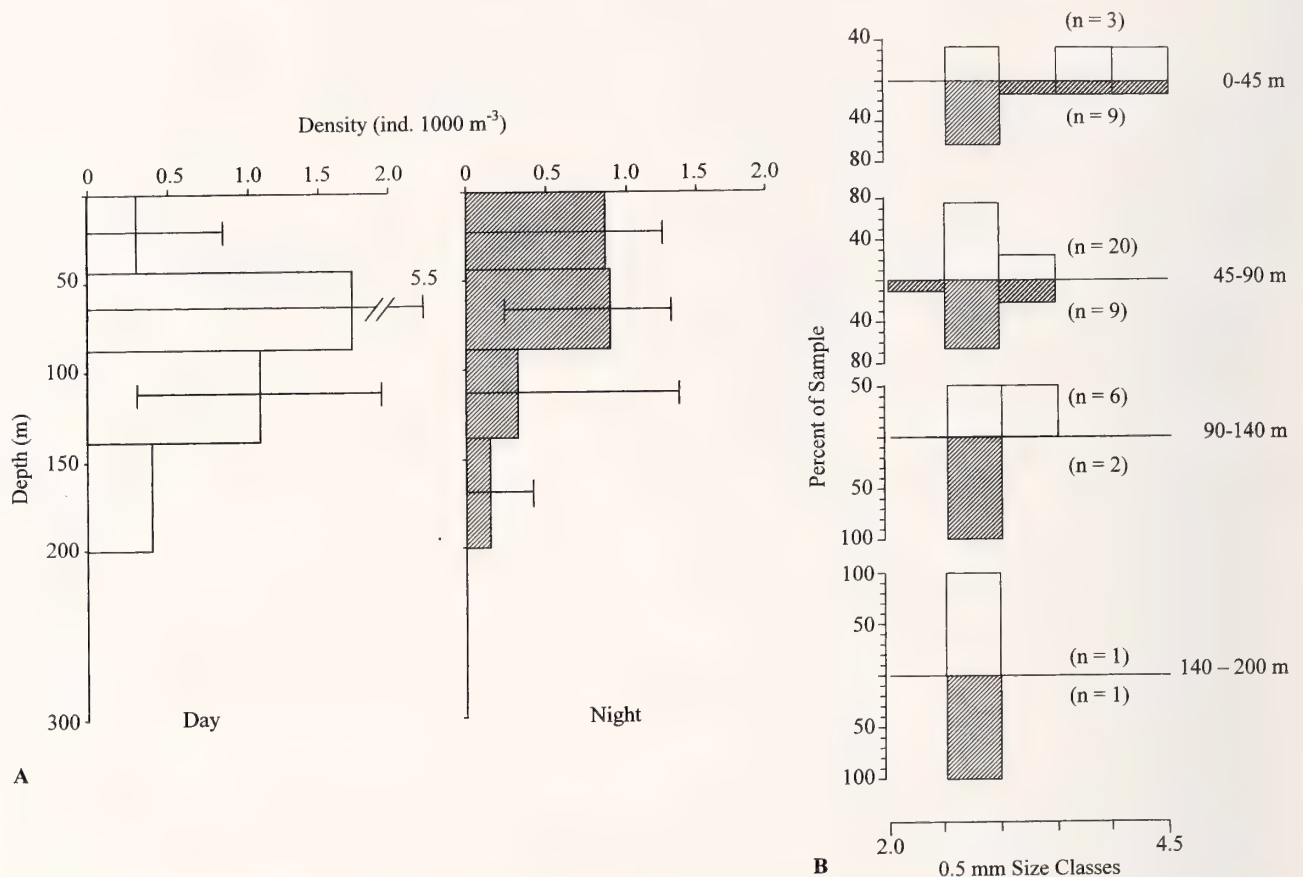


Figure 6. *Diacavolinia angulosa*. Legend as for Figure 4.

extended to about 65 m, below which the temperature decreased steadily to about 10°C at about 300 m and about 6°C at 500 m.

Plankton samples were fixed in 4% buffered seawater-formalin for 48 hr, after which they were transferred to 40% isopropanol. All euthecosomes were removed from the samples. Species identifications were based primarily on Bé and Gilmer (1977), van der Spoel (1967), and van der Spoel et al. (1997); for details see Nigro (2002). One species of *Creseis* was not described in the literature and is referred to here as *Creseis* sp.

Each species was enumerated using a Wild M5A stereomicroscope and the counts were converted to density values expressed as individuals per 1000 m³ (ind. 1000 m⁻³). The species densities of the port and starboard nets for each tow were calculated separately and then averaged. Day and night density data were compared by means of Poisson regression analysis using the SAS version 8.01 statistical package. For each species an interaction effect was assessed between depth and diel period. For each species with a significant interaction, differences between day and night densities were compared within each depth interval.

Shell sizes were determined using the aforementioned

stereomicroscope fitted with a calibrated ocular micrometer. In a given sample, all individuals belonging to a species were measured if the number was less than 100. For those species that occurred in numbers greater than 100 per sample, at least 100 randomly selected individuals were measured (see Nigro, 2002).

Shell diameters were measured for most species in the Family Limacinidae, as the shells in this family are coiled and increase in diameter with growth. Diameters were measured from the outside margin of the aperture to outside of the last whorl with the shell apex in an upward direction. For *Limacina bulimoides*, however, shell length was used instead of diameter because length is greater than diameter in this species (Figure 3) and, thus, is a better indicator of shell size. For species in the Family Cavoliniidae, shell lengths were measured from the posterior to the anterior margins of the shells (Figure 3). For identification purposes, the posterior angle for some *Creseis* spp. and caudal fold width for *Diacavolinia* sp. was measured (Figure 3).

Size-frequency distributions were constructed within each depth interval for each species. Mean sizes were compared between day and night periods within each depth interval by one-way ANOVA using Minitab

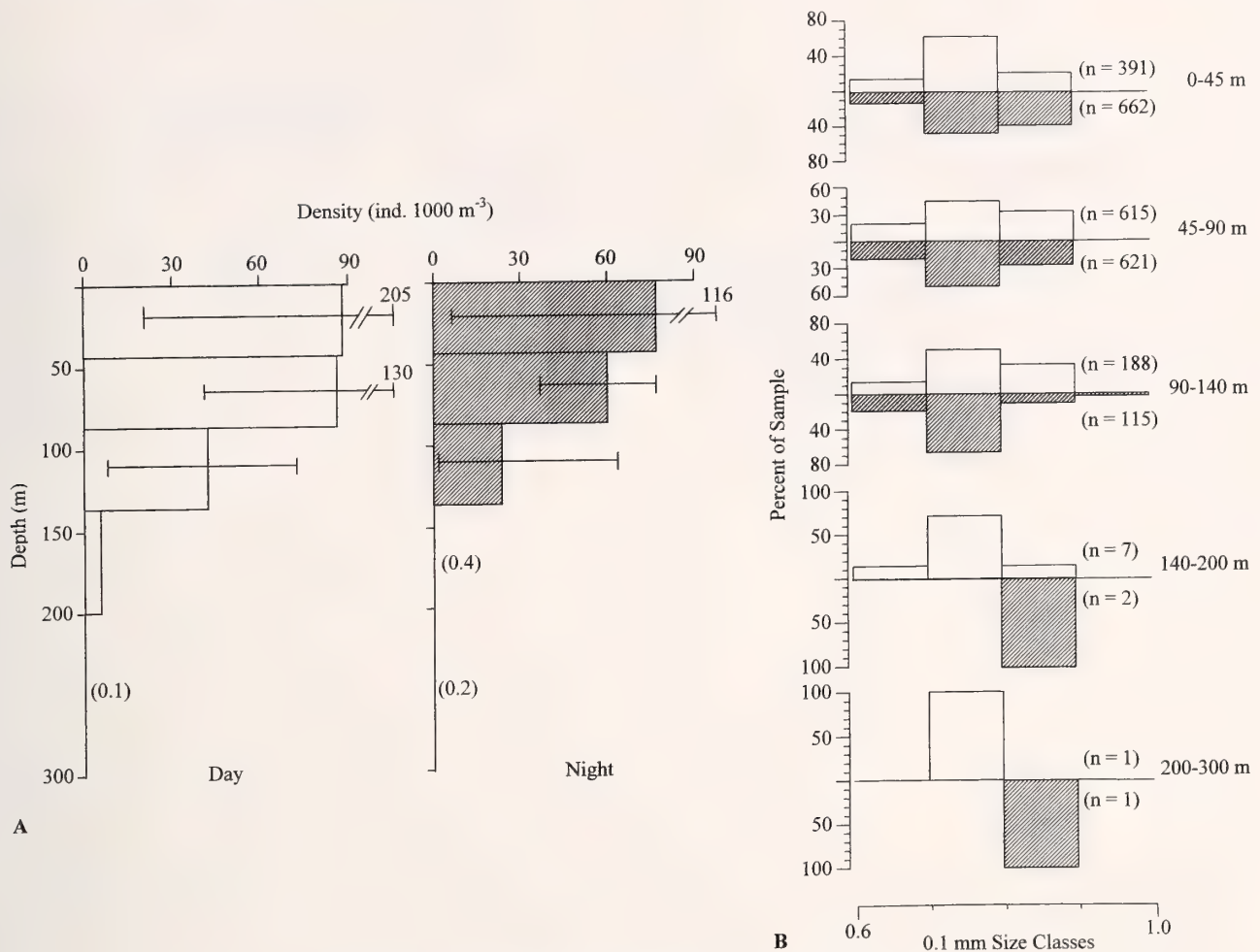


Figure 7. *Limacina trochiformis*. Legend as for Figure 4.

version 9.0. Tukey's option was used to correct the error rate since multiple comparisons of means were made.

After completion of the present study, the sample residues were transferred to the Marine Biodiversity Processing Center of the Los Angeles County Museum of Natural History where they are housed under "Hawaiian Bongo Net Collection" (<<http://collections.nhm.org/collection.html?code=bongo>>).

RESULTS

Water column densities (number of individuals beneath 100 m² of ocean surface) were computed for each species during day and night periods (Table 1). The combined nighttime density for all species (4388 ind. 100 m⁻²) was nearly two and one-half times greater than the total daytime density (1777 ind. 100 m⁻²). Three species (*Limacina inflata*, *Styliola subula*, and *L. trochiformis*) had densities of 1515 to 734 ind. 100 m⁻²,

and together represented 68% of the total nighttime density. Eight species (*Limacina bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa* (Gray, 1850), *Limacina lesueuri*, *Creseis* sp., *Cavolinia inflexa* (Lesueur, 1813), and *Creseis virgula* (Rang, 1828) *conica* Eschscholtz, 1829) had nighttime densities between 409 and 45 ind. 100 m⁻², comprising 30% of the total. The last eight species had nighttime densities of less than 19 ind. 100 m⁻², making up the remaining 2% of the total.

The water column densities during day and night periods were compared by χ^2 analysis (Table 1). Nine of the eleven species with the highest total mean nighttime densities (>45 ind. 100 m⁻²) showed significant diel differences. Only one of those that were significantly different, *Limacina trochiformis*, was more abundant during the day. A total of five species showed no significant diel differences, and five species were collected only at night.

Based on the above results, each species was placed

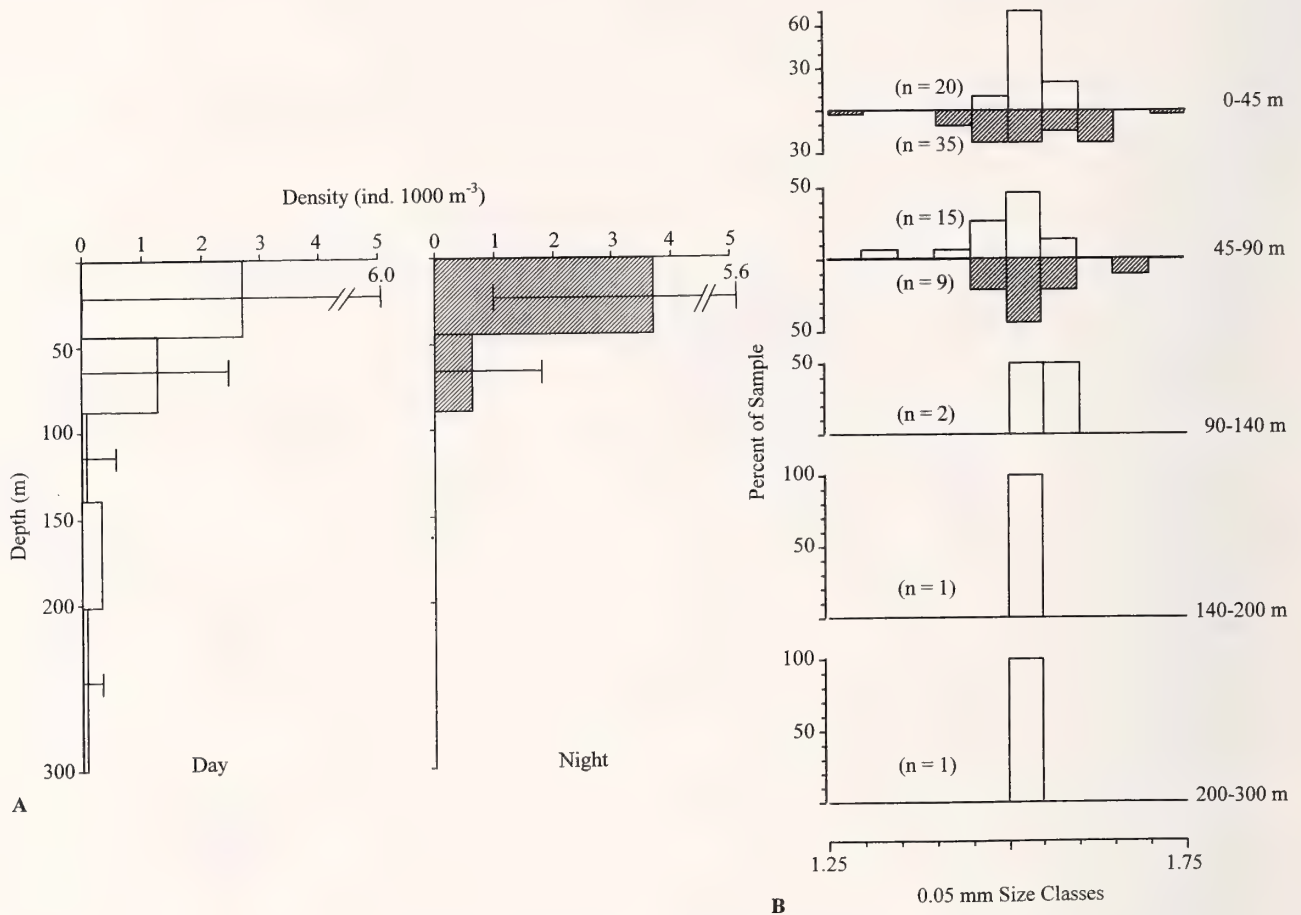


Figure 8. *Diacria danae*. Legend as for Figure 4.

into one of two vertical daytime groupings (Table 1, last column). The first group (epipelagic) was composed of those species present in comparable densities during both day and night periods with the exception of one, *Limacina trochiformis*, which was captured in significantly greater numbers during the day. The second group (epipelagic/mesopelagic and mesopelagic) is inferred from the results and, therefore, is hypothetical because samples were not collected from the mesopelagic zone. This group consisted of species that were either present in the epipelagic zone in significantly higher numbers during the night or were absent from the daytime samples. Individual depth interval means and tests for significance for each species in the two groups are summarized in Nigro (2002).

Epipelagic Species Group

Three species (*Creseis* sp., *C. virgula conica*, and *Diacavolinia angulosa* (Eyedoux and Souleyet, Ms.)(Gray, 1850)) had water column densities that were comparable between day and night (Table 1) and

were restricted to the upper 200 m. For *Creseis* sp., all but four specimens (in the daytime 140–200 m samples) were collected in the upper 140 m (Figure 4A). Individuals in the 0–45 m interval were found only at night, and a significantly greater mean nighttime density was found in the 45–90 m interval. The sum of the mean densities below 90 m was about twice as great during the day than at night, but the difference was not significant. Shell lengths ranged from 1.0 to 3.5 mm (Figure 4B), and no significant differences were found between diel periods.

Creseis virgula conica was limited to the upper 90 m during the day and night (Figure 5A), except for two individuals captured in the nighttime 90–140 m samples. Replicate variability was high above 90 m during both diel periods. Higher daytime densities were recorded from both the 0–45 and 45–90 m depth intervals, but the differences were not significant. Shell lengths ranged from 1.0 to 6.0 mm (Figure 5B). Mean shell lengths were similar in the 0–45 interval, but were significantly greater at night than during the day in the 45–90 m interval.

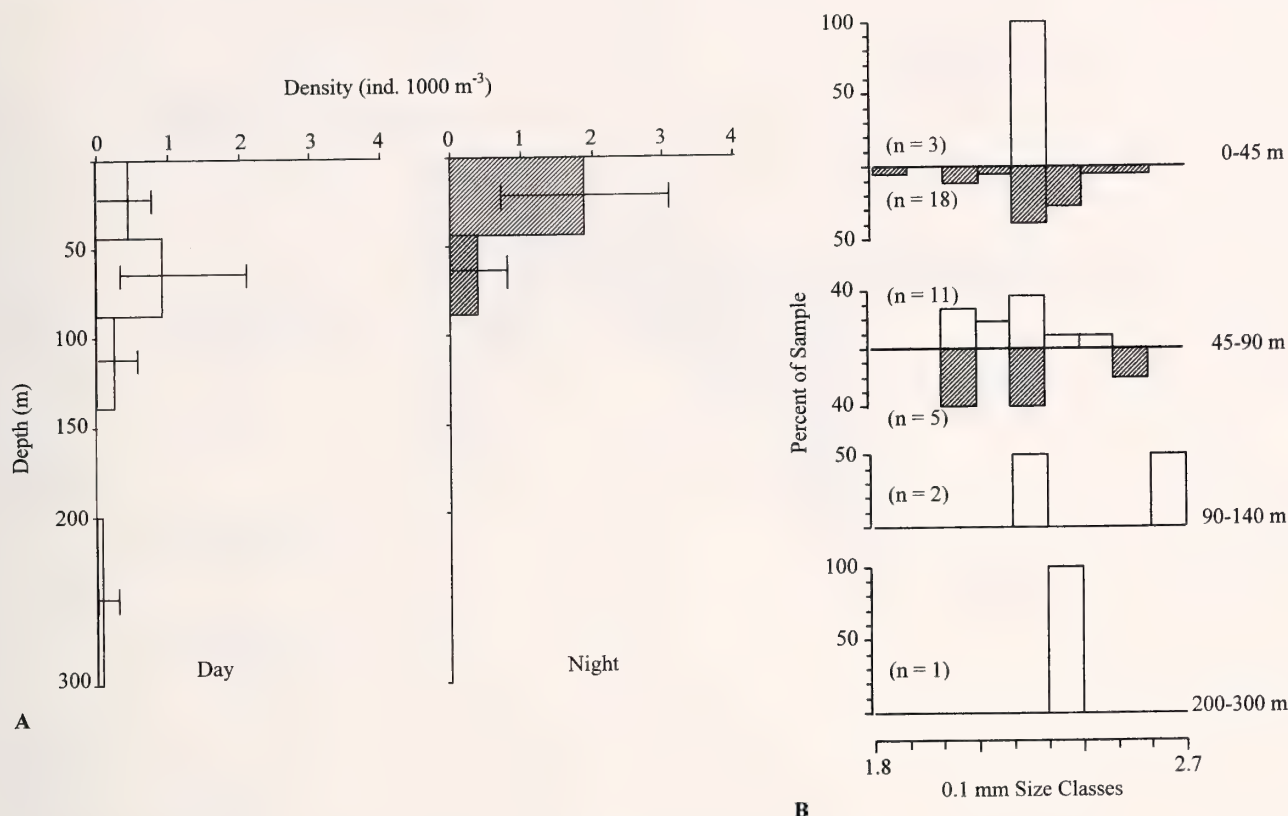


Figure 9. *Diacria costata*. Legend as for Figure 4.

Diacavolinia angulosa was recorded in waters above 200 m during both day and night periods (Figure 6A). Mean densities were low (<2 ind. 1000 m⁻³) with high replicate variability and no significant differences between diel periods. Shell lengths ranged from 2.0 to 4.5 mm and did not differ significantly between day and night periods, although the largest individuals (>3.5 mm) were taken only from the upper 45 m (Figure 6B).

Three species (*Limacina trochiformis*, *Diacria dane* van der Spoel, 1968, and *D. costata* Pfeffer, 1879) had daytime water column densities that were similar to their nighttime densities except for *L. trochiformis*, which had greater densities during the day (Table 1), and extended to 300 m. *Limacina trochiformis* was most abundant above 90 m, with lower densities in the 45–90 m interval and low to very low densities extending down to 300 m (Figure 7A). Replicate variability was high with daytime densities higher in all depth intervals above 200 m, but the diel differences were not significant. Shell diameters ranged narrowly between 0.6 and 1.0 mm (Figure 7B). A significantly larger mean shell diameter was found at night in the 0–45 m interval, but the small (0.02 mm) difference was probably biologically meaningless.

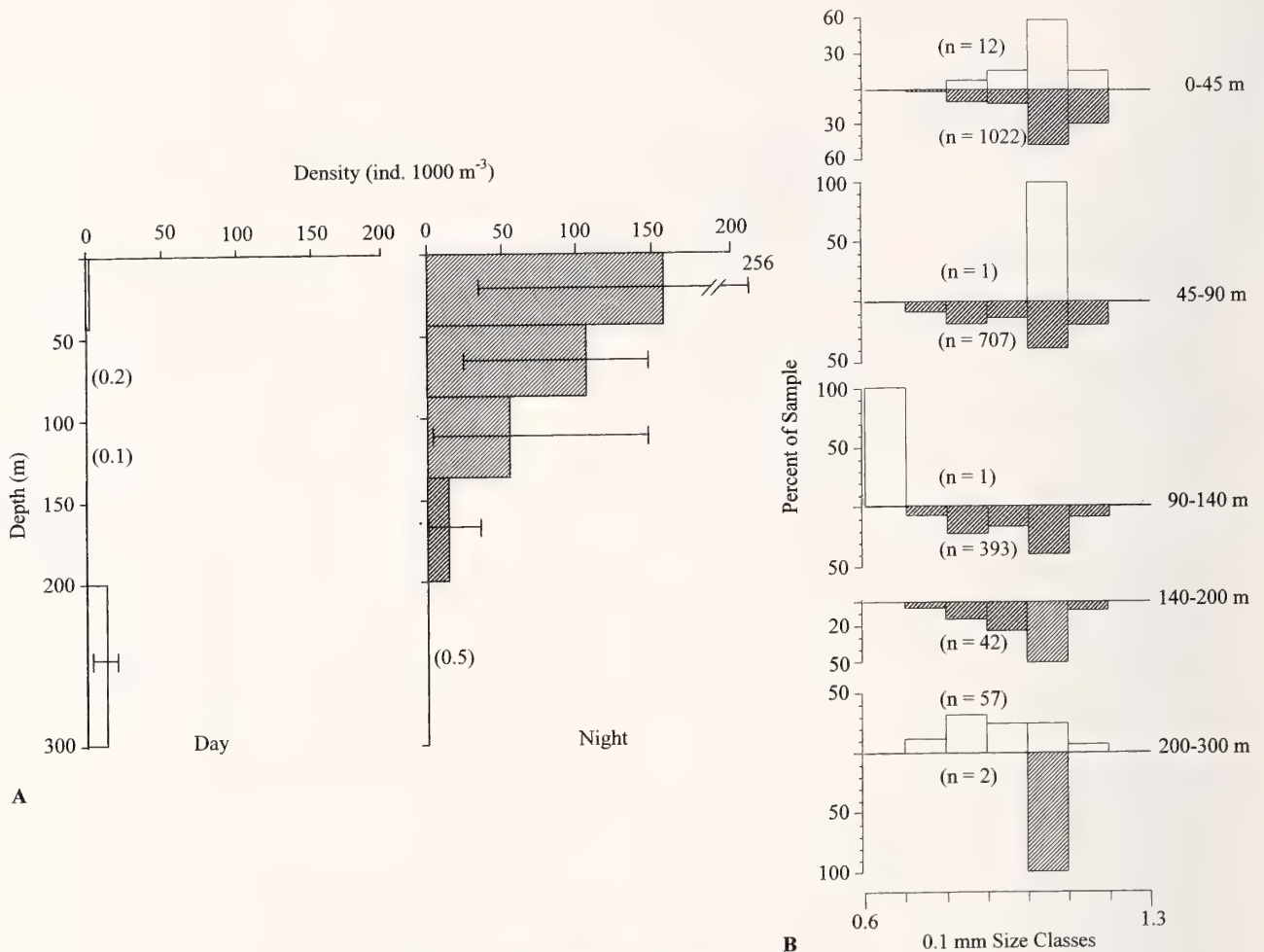
Diacria danae was found from the surface to 300 m during the day and was limited to the upper 90 m at

night (Figure 8A). Maximal densities were found above 45 m during both day and night periods. Variability was high among replicates, with no significant differences in density between diel periods. Shells ranged narrowly between 1.25 and 1.75 mm (Figure 8B). The largest individuals (>1.60 mm) were found only in night samples, but diel differences were not significant.

Diacria costata ranged from the surface to 300 m during the day and was restricted to the upper 90 m at night (Figure 9A). During the day, the majority of individuals were found in the 45–90 m interval, and in the 0–45 m interval at night. Nighttime densities were significantly higher compared to the day in the 0–45 m depth interval. Although daytime densities in the 45–90 m interval were about three times higher than at night, the difference was not significant. Shell sizes ranged from 1.8 to 2.7 mm (Figure 9B) and were comparable between diel periods in the 0–45 and 45–90 m depth intervals.

Epipelagic/mesopelagic and Mesopelagic Species Group

Eight species (*Limacina inflata*, *Styliola subula*, *L. bulimoides*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa*, *L. lesueuri*, and *Cavolinia inflexa*) had

Figure 10. *Limacina inflata*. Legend as for Figure 4.

daytime water column densities that were significantly lower than nighttime densities in the upper 300 m (Table 1). These species are hypothesized to be daytime occupants of the epipelagic/mesopelagic and mesopelagic zones.

Limacina inflata was captured from surface waters to 300 m during both diel periods (Figure 10A), except that it was absent from 140–200 m during the day. At depths above 200 m it was recorded in very low numbers during the day. At night replicate variability was high, and significantly greater numbers were captured above 140 m with a maximum in the 0–45 m depth interval. No significant diel differences were found below 140 m, although the mean daytime density in the 200–300 m interval was 17 times greater than at night. Shell diameters ranged from 0.6 to 1.3 mm, and were not significantly different in the 0–45 m interval (Figure 10B). Small sample sizes ($n \leq 2$) in deeper intervals from either day or night periods prohibited statistical comparisons.

Styliola subula was present in low to very low numbers above 200 m during the day, and it was restricted to the upper 200 m at night (Figure 11A). It exhibited high replicate variability at night and increased from low numbers at 140–200 m to a maximum in the upper 45 m. Significantly greater densities were found only at night in depth intervals above 140 m. The mean nighttime density at 140–200 m was higher than during the day, but the difference was not significant. Shell lengths ranged broadly from 1.0 to 9.0 mm. No significant differences in shell sizes (Figure 11B) were found, although individuals larger than 5.0 mm were taken only from night samples.

Limacina bulimoides was captured from surface waters to 300 m during the day with density increasing with depth, and it was mainly found in the upper 140 m at night (Figure 12A). Nighttime densities were significantly greater compared to the day in depths above 140 m. Replicate variability was high at night with

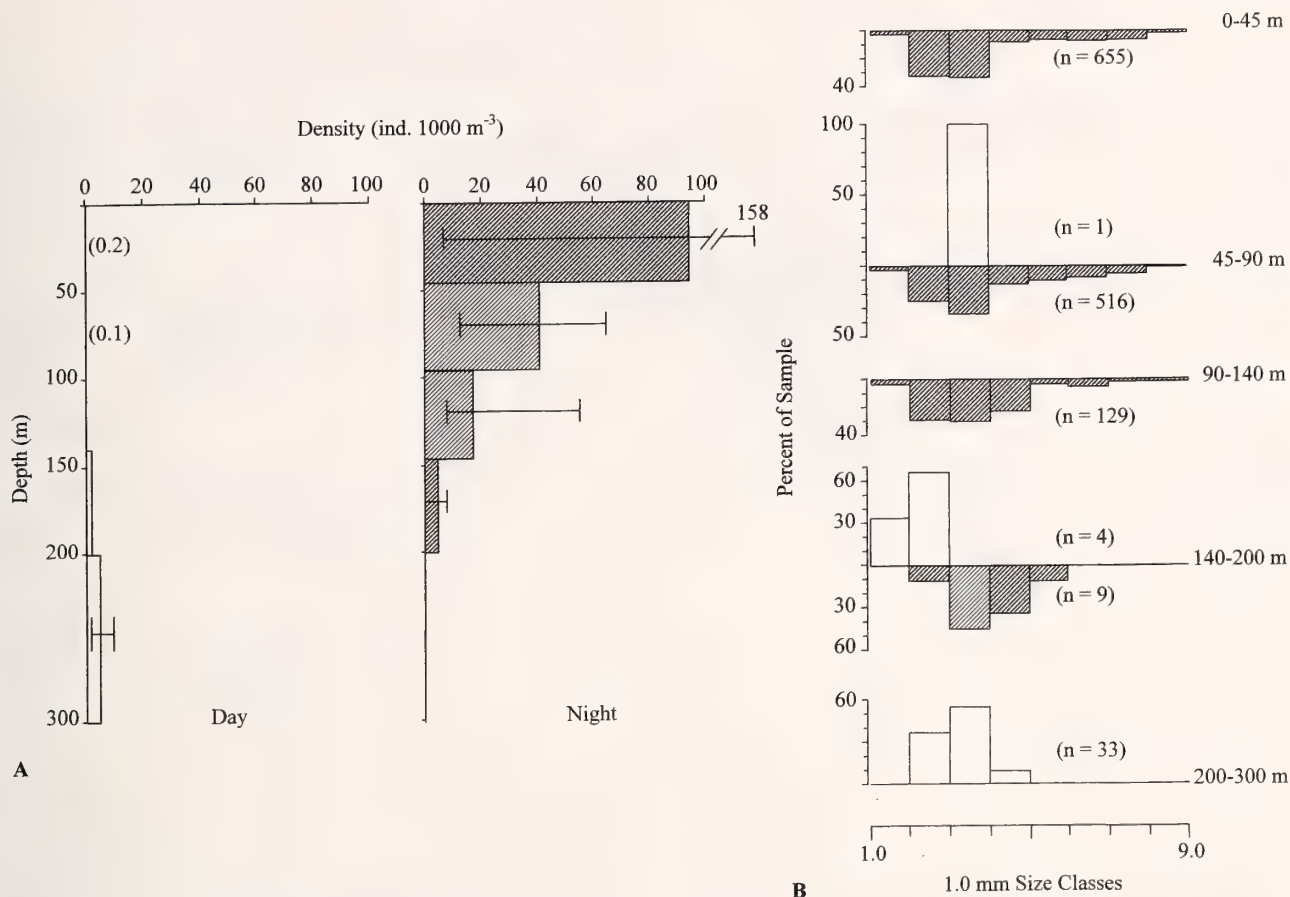


Figure 11. *Styliola subula*. Legend as for Figure 4.

densities increasing from a low at 140–200 m to a maximum at 0–45 m. The mean daytime density between 140 and 200 m was higher than at night, but the difference was not significant. Shell lengths ranged narrowly from 0.6 mm to 1.6 mm and were significantly larger at night in the 90–140 m depth interval (Figure 12B). In waters above 90 m, the largest individuals (>1.4 mm) were taken only at night.

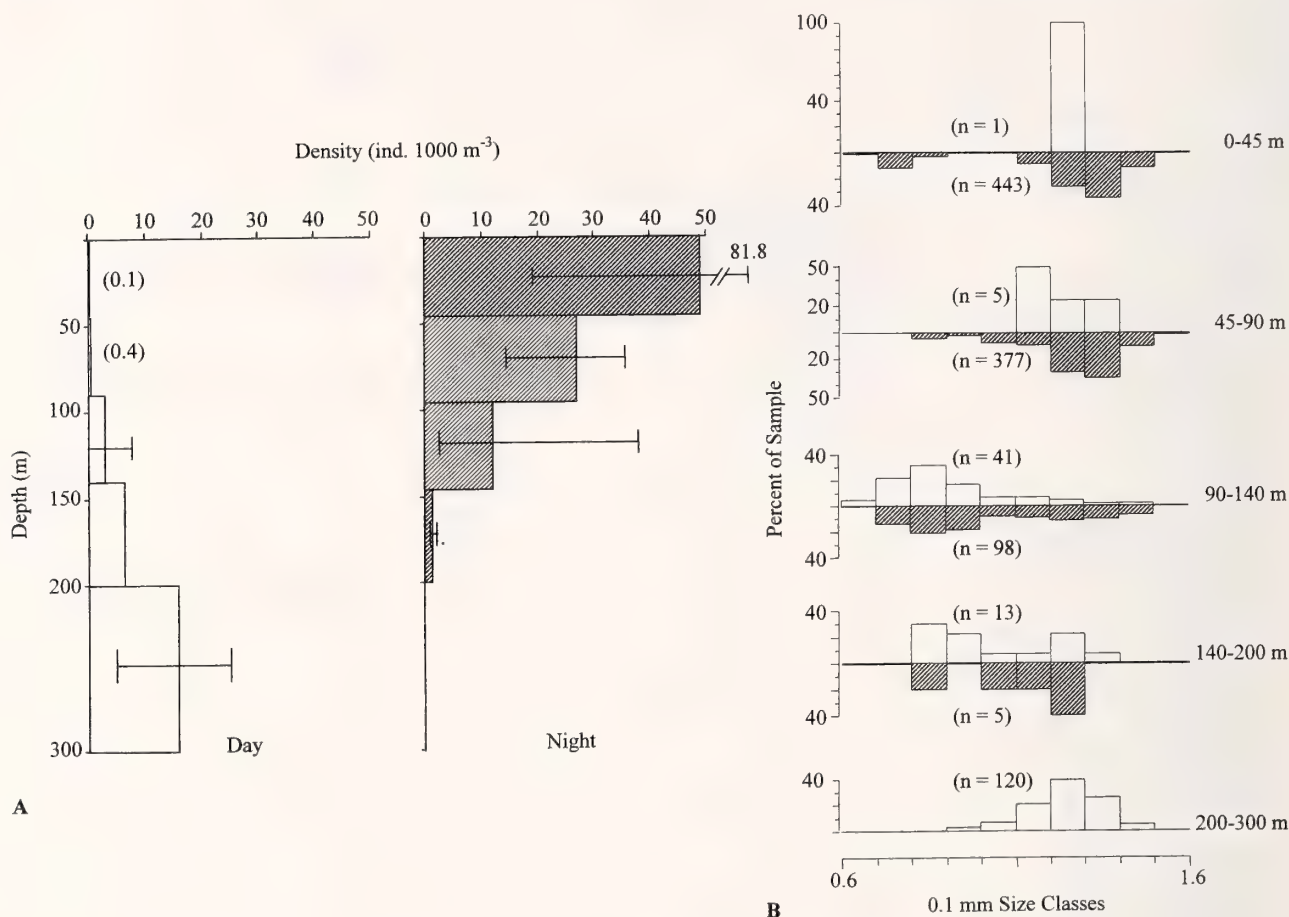
Creseis acicula was present in low numbers from the surface to 300 m during the day and was restricted to waters above 200 m at night, although it was only abundant above 90 m (Figure 13A). High replicate variability was found among the night tows above 90 m. Nevertheless, nighttime densities were significantly greater than daytime densities in the 0–45 and 45–90 m intervals. Most (80%) of those individuals captured at night were in the 0–45 m interval. Shell lengths ranged broadly from 2.0 to 9.0 mm (Figure 13B) with no significant diel differences, except in the 45–90 m interval where the mean length was significantly larger at night.

Clio pyramidata was absent from waters above 140 m and was scarce (mean abundances < 1.0 ind.

1000 m⁻³) between 140 and 300 m during the day (Figure 14A). At night, this species was present only above 200 m with a maximal density in the 90–140 m interval. The total mean nighttime density was 20 times greater than during the day. Shell sizes varied widely from 1.0 to 13.0 mm (Figure 14B). Only the smallest shells (1.0–2.0 mm) were recorded from day tows. Large shells (>7.0 mm) were all recorded from night tows in the upper 90 m.

Cavolinia globulosa was present down to 140 m during the day and to 300 m at night (Figure 15A). Mean nighttime densities were significantly greater than daytime densities in the 0–45 m interval and significantly less in the 45–90 m interval. No significant differences were found below 90 m. Shell lengths ranged broadly from 0.5 to 6.5 mm and were significantly greater at night in all depth intervals above 140 m (Figure 15B). Large individuals (>3.5 mm) were collected only at night from tows above 200 m, except for one shell (5.5 mm) collected during the day from the 90–140 m interval.

Limacina lesueuri was present in very low numbers (<0.3 ind. 1000 m⁻³) between the surface and 300 m

Figure 12. *Limacina bulimoides*. Legend as for Figure 4.

during the day and was recorded in increasing numbers from 200 m to the 0–45 m interval at night (Figure 16A). Total mean nighttime densities were 52 times greater than daytime densities. Sixty-three percent of those captured at night were from the 0–45 m interval. Shell sizes ranged narrowly from 0.7 to 1.3 mm (Figure 16B) with the largest (>1.2 mm) captured only at night above 140 m. Many zero density samples prevented statistical comparison of density and size distributions.

Cavolinia inflexa was captured down to 300 m during the day and to 200 m at night (Figure 17A). Although slightly higher mean densities were recorded in all depth intervals at night, no significant differences were found, most probably due to the high replicate variability. Shells lengths ranged broadly from 1.0 to 6.0 mm. Those >2.5 mm were found only in the upper 140 m at night (Figure 17B), and individuals from the intervals above 90 m were significantly larger at night.

Five species (*Cuvierina columnella* (Rang, 1827), *Hyalocylis striata* (Rang, 1828), *Diacria maculata* Bleeker and van der Spoel, 1988, *Cavolinia gibbosa*

(d'Orbigny, 1836), and *D. major* (Boas, 1886)) were absent from the upper 300 m during the day (Table 1). These species are hypothesized to be daytime occupants of the mesopelagic zone. Except for *Cuvierina columnella* and *Hyalocylis striata*, which were captured in moderate to low numbers at night, the remaining three were captured in extremely low numbers at night and were not recorded from day tows. *C. columnella* was captured in the upper 200 m (Figure 18A), and most individuals (64%) were recorded from the 0–45 m interval. Shell lengths ranged narrowly between 7.0 and 8.0 mm (Figure 18B) with the largest individuals (>7.6 mm) between 45 and 90 m.

Hyalocylis striata was recorded only in waters above 90 m at night (Figure 19A). Mean densities were low (<1.0 ind. 1000 m⁻³) and nearly the same in the 0–45 and 45–90 m intervals. Shell length ranged from 2.5 to 7.0 mm (Figure 19B) with shells larger than 3.5 mm taken only from the 45–90 m interval.

Diacria maculata and *D. major* were captured in extremely low numbers (five and one individuals, respectively) above 140 m at night. Sizes were not

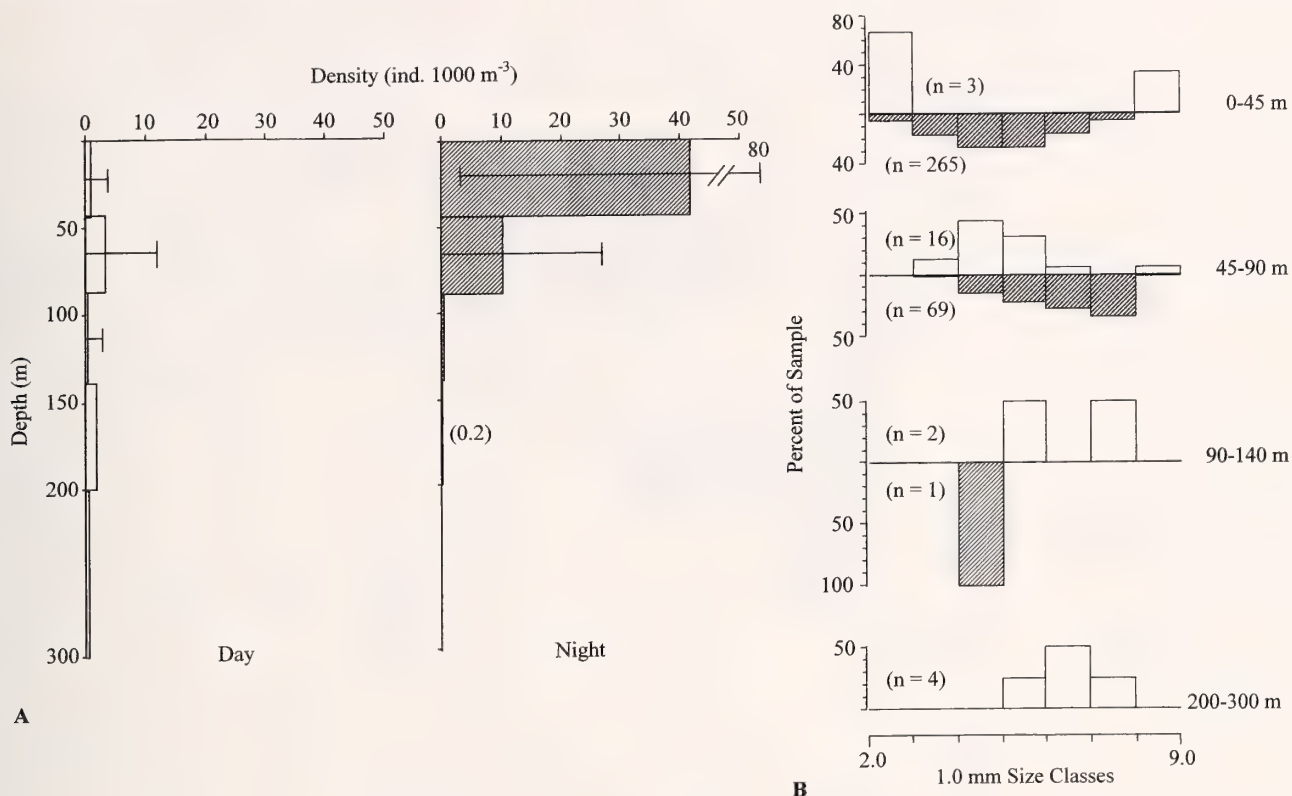


Figure 13. *Creseis acicula*. Legend as for Figure 4.

measured, as all shells were broken to some extent making size estimation unreliable. Lastly, a single *Cavolinia gibbosa* with a shell length of 9.2 mm was captured at night from the 200–300 m depth interval.

DISCUSSION

Based on the reviews of euthecosome taxonomy and biogeography by van der Spoel (1967), Bé and Gilmer (1977), and van der Spoel et al. (1997), and two subsequent taxonomic studies (van der Spoel and Pierrot-Bults, 1998 and Bontes and van der Spoel, 1998), 68 species of euthecosomes are currently recognized from the world's oceans. Half (34) have been reported from the tropical and/or subtropical Pacific Ocean (Table 2). McGowan (1960, 1963, 1971) identified 18 species with distributions that coincide with Hawaiian waters, all of which were collected in the present study with two exceptions. The first, *Cavolinia uncinata* (Rang, 1829), was classified as a tropical species by Bé and Gilmer (1977) and may be limited to lower latitudes south of the Hawaiian Islands. The second, *Cavolinia tridentata* (Neibuhr, 1775), was classified as subtropical and uncommon by Tesch (1948) and McGowan (1960).

Of the 19 species identified from the upper 300 m of the water column in the present study, 8 were present in

significantly greater numbers at night than during the day while 5 were collected only at night, and, by implication, were below 300 m during the day. The most probable explanation for the difference in day-night densities for these 13 species is nocturnal vertical migration.

If a major adaptive value for nocturnal vertical migration is reduced visibility to visual predators during the day, then the shallowest daytime depths should coincide with that depth at which an individual ceases to present a perceptible visual cue (Angel, 1985). Off Hawaii, the shallowest daytime depth at which counterillumination can occur is 400 m, which coincides with the shallowest daytime depth of midwater micronekton (Young et al., 1980). This depth also should coincide with the shallowest daytime depth for mesopelagic euthecosomes and could explain the absence or low abundance during the day of the 13 species above 300 m in the present study. An alternate hypothesis explaining differences in density between day and night periods is the ability of animals to avoid an oncoming plankton net during the day.

Daytime net avoidance was hypothesized by McGowan and Fraundorf (1966) to be a function of net size. They found that 20- and 40-cm diameter nets (0.03 and 0.13 m²) underestimated euthecosome abundances obtained with a 140-cm net (1.54 m²). Nets with diameters

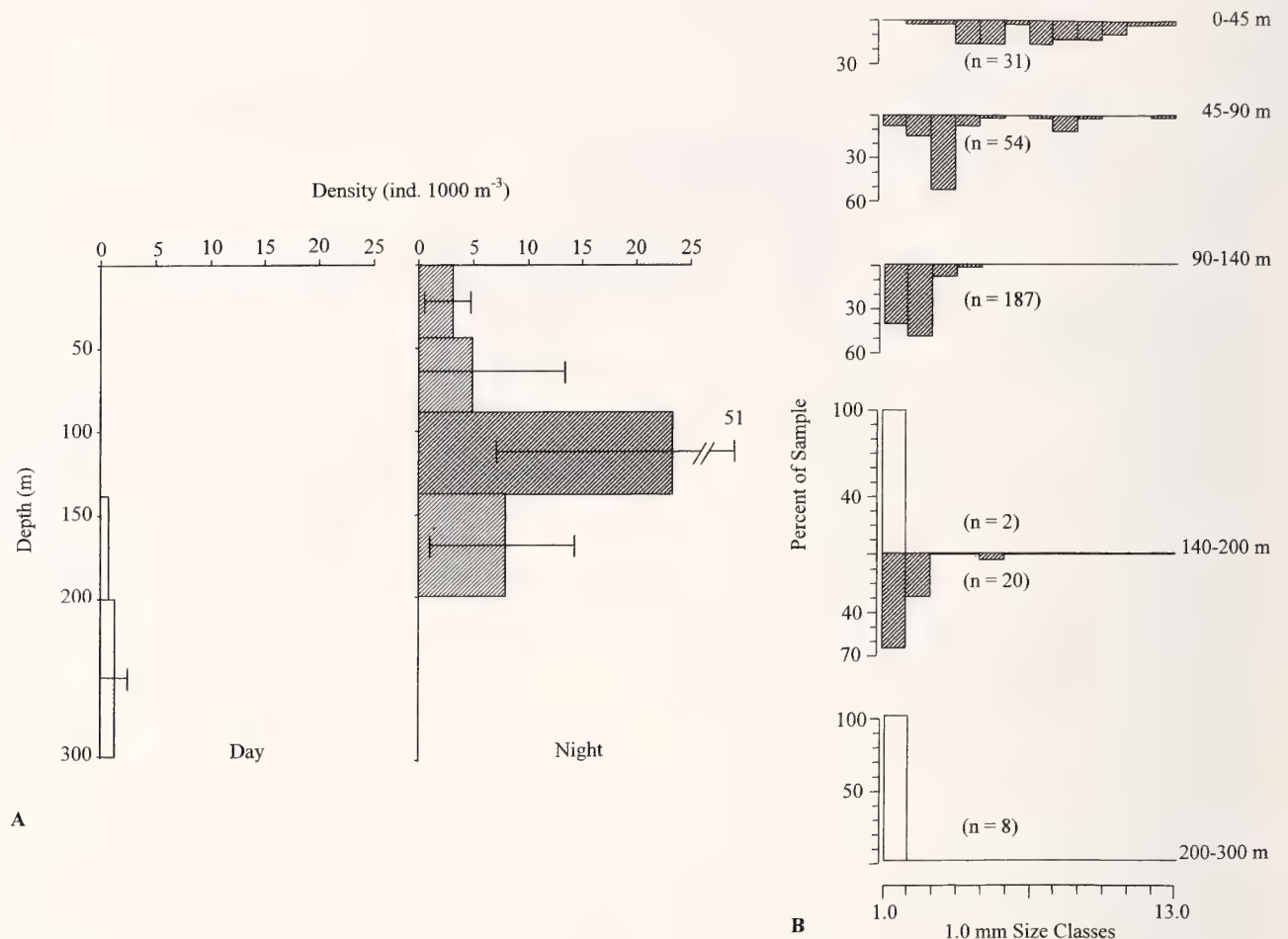


Figure 14. *Clio pyramidata*. Legend as for Figure 4.

of 60, 80 and 100 cm (0.28, 0.50, and 0.79 m²) gave intermediate results. Hypothetically, net avoidance of the 70-cm Bongo nets used here should be comparable with that obtained with their 60- and 80-cm nets. However, the paired 70-cm Bongo nets have unobstructed mouth openings while the individual nets used by McGowan and Fraundorf employed three-point towing bridles.

Strong support for an hypothesis that diel differences in density of euthecosomes at epipelagic depths are due to vertical migration and not net avoidance is given by data from Wormuth (1981). He compared the density of nine abundant euthecosomes from 22 day and night samples collected from nine discrete depth intervals to 1000 m using a 1-m² multiple open-closing net and environmental sensing system (MOCNESS). Like the Bongo nets, the mouth opening of the 1-m² nets was unobstructed. Wormuth found no significant difference between total species densities from day and night periods. Additional support for the above hypothesis is the lack of eyes or well-developed photoreceptors that

would be sufficiently sensitive to detect a change in light intensity produced by an oncoming net. Euthecosomes do possess one (in Limacinids) or two tentacles with tissue that may serve to detect differences in light intensity (Lalli and Gilmer, 1989). However, their ability to detect an oncoming net is improbable. A tactile function of the tentacles is probable, but such sensory receptors would operate equally as well during the day as at night to invoke net avoidance behavior.

For some species, it is also possible that larger individuals are more capable of daytime net avoidance than smaller ones. In the present study, we found that daytime tows in the upper 300 m collected only small individuals of *Cavolinia inflexa* (<2.5 mm) and *Clio pyramidata* (<2.0 mm), while nighttime tows collected individuals up to 6.0 mm and 13.0 mm, respectively. However, an alternate explanation is that resident daytime populations of small animals reside between the surface and 300 m, while larger individuals are found deeper.

Daytime and nighttime patterns of vertical distribu-

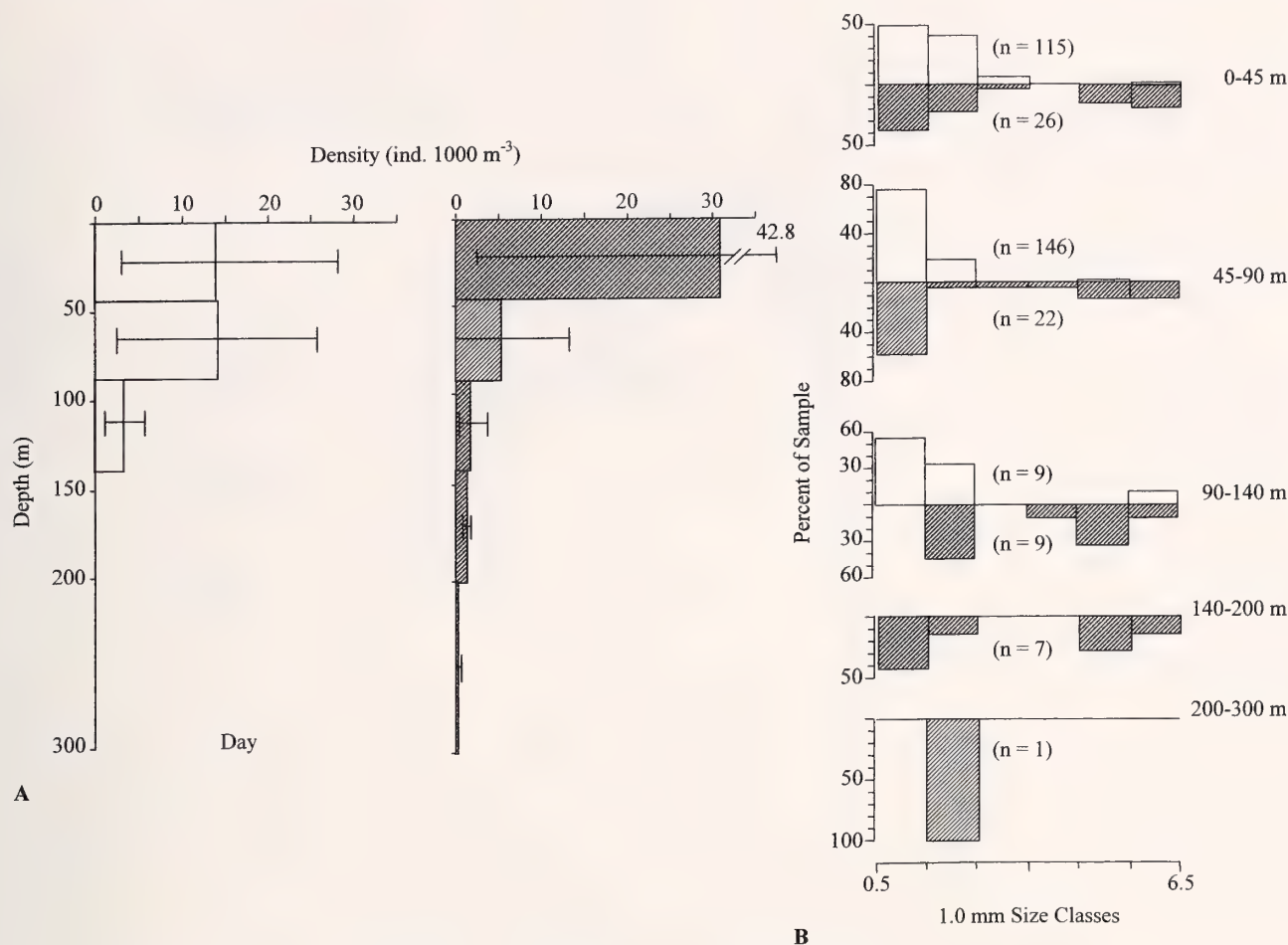


Figure 15. *Cavolinia globulosa*. Legend as for Figure 4.

tion would be expected to differ between localities mainly as a result of differences in light penetration, which is affected by water turbidity and season (at increasingly higher latitudes). Even in some tropical and subtropical areas, water clarity may vary due to seasonal upwelling and river runoff. In the eastern Caribbean, for example, massive freshwater runoff from the Orinoco River can cause dramatic changes in turbidity. This phenomenon has been observed on a seasonal basis far from the river mouth in the waters around Barbados (C. Lalli, personal communication). Secondary causes of variability in the depth of the epipelagic zone include increased turbulence due to storms, variations in light penetration due to atmospheric conditions, and variability in plankton density. For example, the samples used in the present study were collected during a period of seven days in the month of April with clear weather and calm seas. It is reasonable to expect that samples taken during other times of the year of the study may have yielded different results from those reported here. Lacking

information regarding the depth of the epipelagic zone at the localities and times of the previous studies in the North Atlantic (discussed below), the vertical distribution patterns characterized here from Hawaiian waters may or may not be directly comparable. Nonetheless, we decided that we should examine intra-species patterns reported by previous authors whose studies were conducted in the western North Atlantic with the aforementioned aspects serving as an explanatory framework for differences that may occur.

Among the six species classified as epipelagic in the present study, three (*Limacina trochiformis*, *Creseis virgula conica*, and *Diacavolinia angulosa*) showed no evidence of migration, while three (*Creseis* sp., *Diacria danae*, and *D. costata*) performed limited nocturnal migrations. Wormuth (1981) found that *L. trochiformis* and *C. virgula conica* from the Sargasso Sea were non-migrators with peak abundances above 100 m and 200 m, respectively, during both day and night periods. These results are similar to those of the present study, where >50% of the sampled population of *L.*

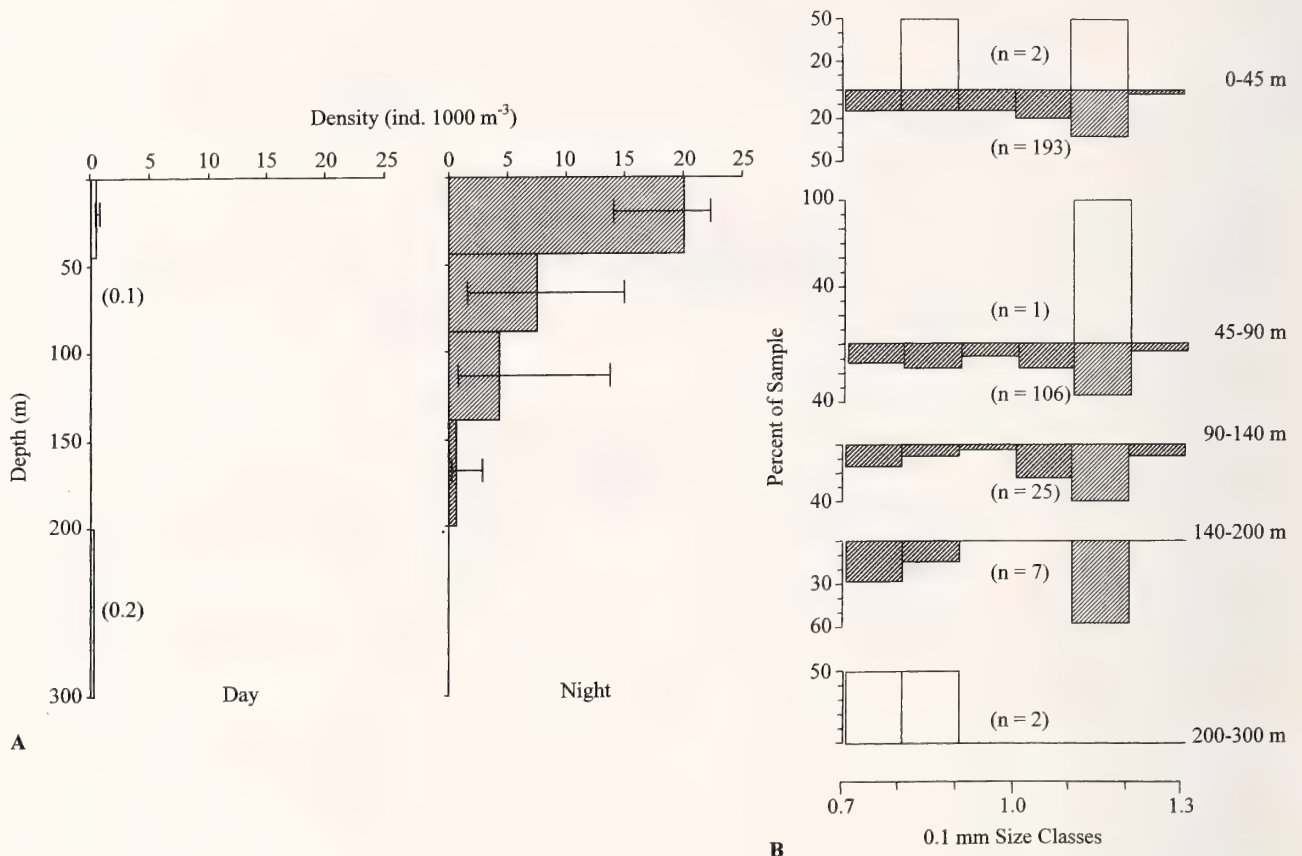


Figure 16. *Limacina lesueurii*. Legend as for Figure 4.

trochiformis was in the upper 140 m and no individuals of *C. virgula conica* were found below 140 m during either diel period. Downward nocturnal migration from the surface by adults of *C. virgula conica* in the Caribbean were reported by Haagensen (1976). There may be some evidence of this pattern in the present study, as nighttime densities were somewhat lower than daytime densities above 90 m.

The vertical distribution of "*Cavolinia longirostris*" was reported by Wormelle (1962). She found evidence of migrations in the Florida Current with 50% of the individuals above 219 m during the day and above 76 m at night. In contrast, Chen and Bé (1964) found no diel differences in surface waters (0–10 m) in the western North Atlantic. Comparison of these results with the present is not possible because "*C. longirostris*" was split into 24 species by van der Spoel et al. (1993). One of these species, *Diacavolinia angulosa*, was identified in the present study. Which species (or multiple species) was represented by "*C. longirostris*" in Wormelle's study is not known.

Our results for *Diacria danae* and *D. costata* can be compared indirectly with three reports for *D. quadridentata* (de Blainville, 1821), which may actually

represent one or both of the above species (discussed in Nigro, 2002). Off Hawaii, *D. danae* showed a pattern that was nearly identical to *D. costata*, remaining exclusively in the upper 140 m during both diel periods. There was some evidence of migration by individuals dwelling deeper than 90 m during the day to waters above 90 m at night, which is in general agreement with patterns found in the Caribbean by Haagensen (1976) and in the western North Atlantic by Wormelle (1962). However, in the surface waters of the western North Atlantic, Chen and Bé (1964) found no evidence of migration for *D. quadridentata*.

Ten of the 13 species assigned to the epipelagic/mesopelagic and mesopelagic species group appeared to undergo nocturnal vertical migrations in the present study; three Limacinidae (*Limacina inflata*, *L. bulimoides*, and *L. lesueurii*), and seven Cavoliniidae (*Styliola subula*, *Creseis acicula*, *Clio pyramidata*, *Cavolinia globulosa*, *Cavolinia inflexa*, *Cuvierina columella*, and *Hyalocylis striata*). These species were either absent or present in low numbers in the upper 300 m during the day and in moderate to high numbers in the upper 140 m at night.

Wormuth (1981) recorded *L. inflata* down to

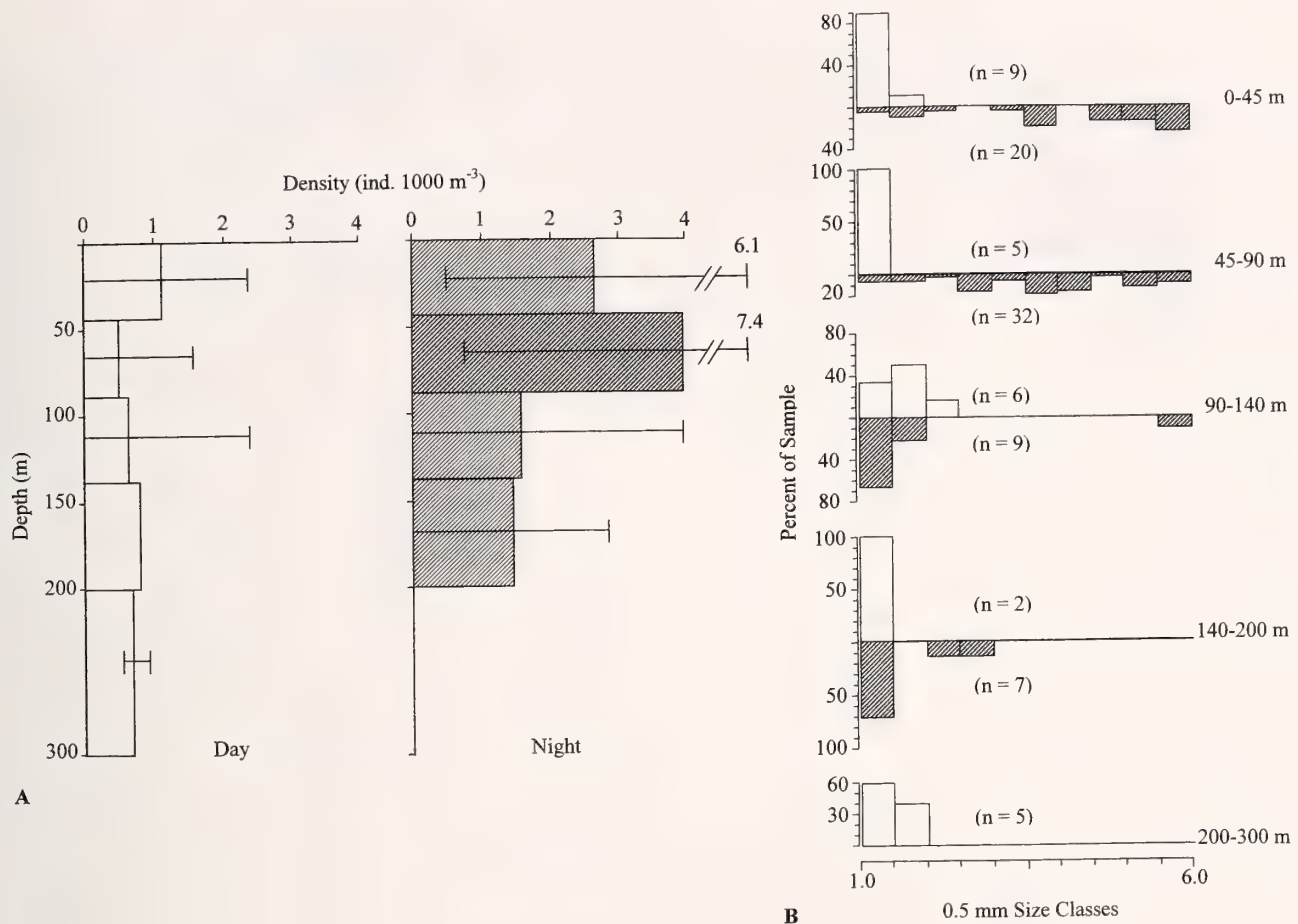


Figure 17. *Cavolinia inflexa*. Legend as for Figure 4.

≥ 1000 m in the Sargasso Sea during the day with peak densities between 100 and 400 m. He found most of the individuals at night in the upper 75 m with a gradual decrease in numbers down to 125 m. In the present study, the total daytime density in the upper 300 m was 3.2% of the nighttime density. Assuming that night tows are a reasonable estimate of population density and that daytime net avoidance is either absent or not significant, then only 3.2% of the population occurred above 300 m during the day whereas $>50\%$ were found at depths above 100 m at night. These data correspond generally with the results described above from Wormuth from the Sargasso Sea. In marked contrast, Wormelle (1962) reported that in the Florida Current 50% of the individuals were captured above 236 m during the day and 232 m at night (i.e., no evidence of nocturnal migration).

Styliola subula and *Limacina bulimoides* were found by Wormuth (1981) to be vertical migrators in the Sargasso Sea, with most of each species population above 100 m at night and above 260 m during the day. In the present study, the water column density of *S.*

subula was 13 times greater at night than during the day (Table 1). Also, most of the specimens from the day samples were 1–3 mm, while those from the night tows ranged from 1–9 mm (Figure 13). These density and size differences suggest nocturnal migration of *S. subula* greater than 3 mm from depths below 300 m. For *L. bulimoides*, there were no diel differences in shell sizes, although in agreement with Wormuth there was an evident nocturnal vertical migration from waters below 140 m during the day to above 140 m at night. Wormuth (1986) reported that shell size increased with decreasing depth in the upper 100 m; most individuals ranged in size from 0.5 to 0.8 mm between 50 and 100 m, 1.2 to 1.4 mm between 25 to 50 m, and 1.3 to 1.5 mm from 0 to 25 m. Comparison of shell sizes in the 0–45 and 45–90 m intervals in our study, however, show no such vertical difference, especially at night where the size-frequency distributions were based on large sample sizes (Figure 14).

Myers (1967) reported maximum concentrations of *Creseis acicula* at night in the upper 50 m off Cape Hatteras, and Wormuth (1981) suggested that some

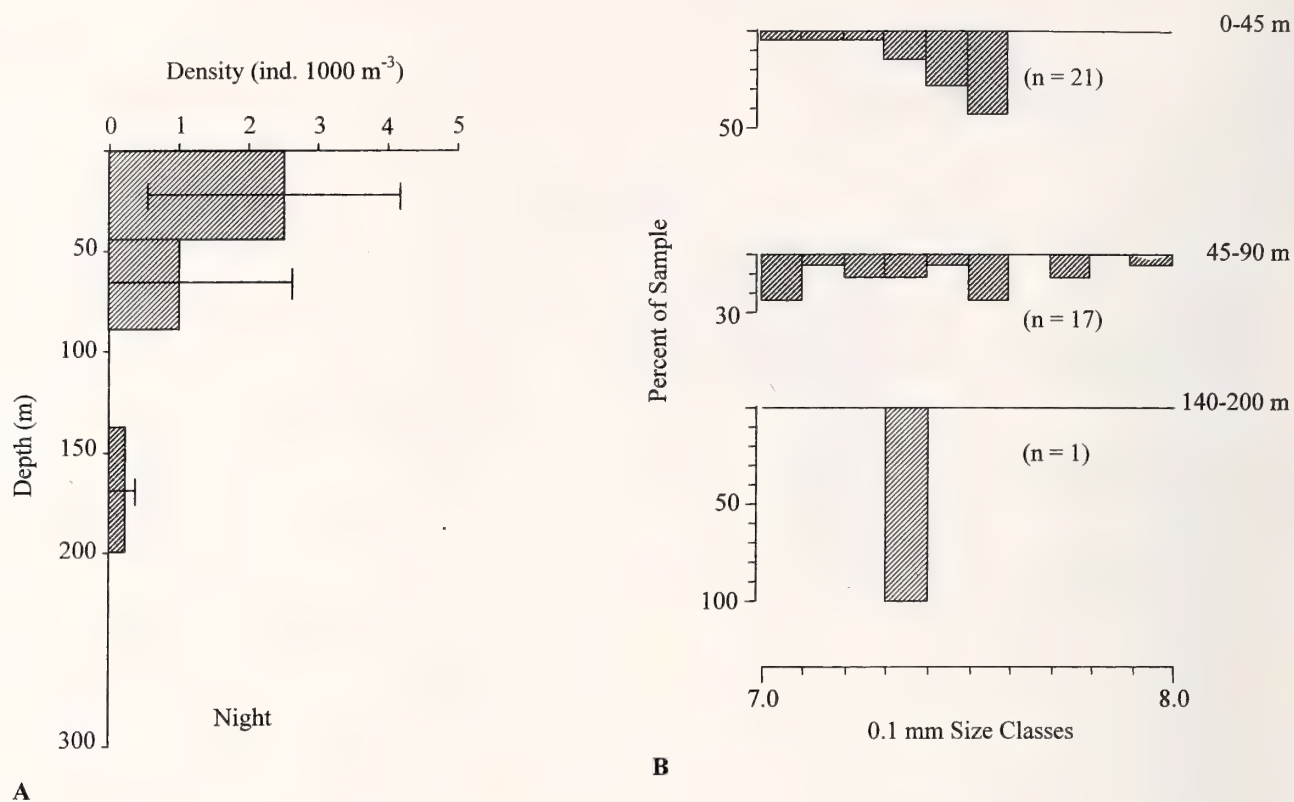


Figure 18. *Cuvierina columnella*. Legend as for Figure 4.

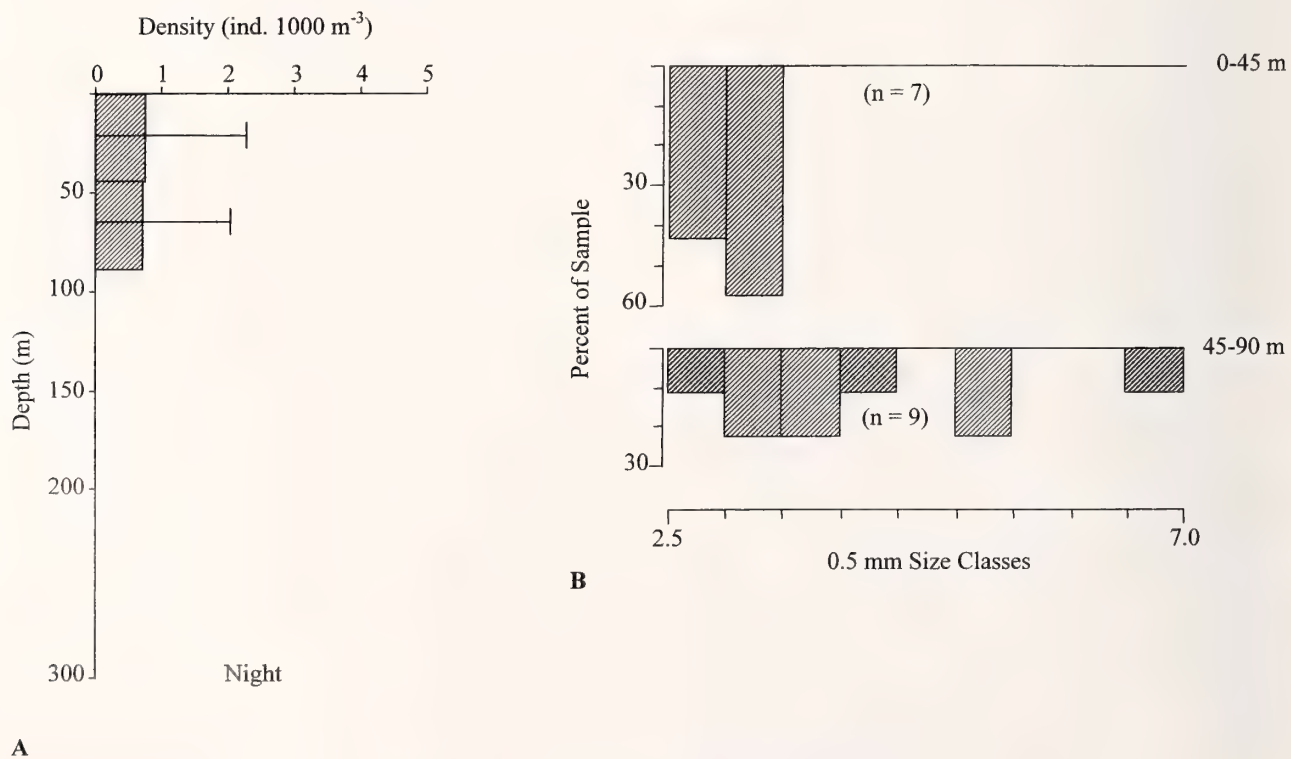


Figure 19. *Hyalocylis striata*. Legend as for Figure 4.

Table 2

Geographic distribution of euthecosomes and comparison of species collected from the North and Equatorial Pacific Ocean by McGowan (1960) and the present study (indicated by asterisks). Only distinct species are listed; for those with known morphological variants (i.e., subspecies, varieties, or formae), the distribution includes all subspecific taxa. Species in bold print have tropical and/or subtropical distributions in the North Pacific Ocean. Sources of data are: 1) Bé and Gilmer (1977), 2) van der Spoel et al. (1993), 3) van der Spoel et al., (1997), 4) Bontes and van der Spoel (1998), and 5) van der Spoel and Dadon (1999). + = present, - = absent.

Species	Biogeographic Region				Source of Data	Mc Gowan (1960)
	Polar	Subpolar	Subtropical	Tropical		
Family Limacinidae						
<i>Limacina bulimoides</i> *	—	—	+	+	3,5	+
<i>Limacina helicina</i>	+	+	—	—	1	+
<i>Limacina helicoides</i>	—	—	+	+	5	—
<i>Limacina inflata</i> *	—	—	+	+	1,3,5	+
<i>Limacina lesueuri</i> *	—	—	+	—	1	+
<i>Limacina retroversa</i>	—	+	—	—	1,5	—
<i>Limacina trochiformis</i> *	—	—	+	+	3,5	+
Family Cavoliniidae						
<i>Cavolinia gibbosa</i> *	—	—	+	—	1	+
<i>Cavolinia globulosa</i> *	—	—	+	+	1	+
<i>Cavolinia inflexa</i> *	—	—	+	+	1	+
<i>Cavolinia tridentata</i>	—	—	+	+	1,5	+
<i>Cavolinia uncinata</i>	—	—	—	+	1	+
<i>Clio andrae</i>	—	—	+	+	5	—
<i>Clio antarctica</i>	—	+	—	—	1	—
<i>Clio balantium</i>	—	—	+	+	1	+
<i>Clio campylura</i>	—	—	—	+	3	+
<i>Clio chaptalii</i>	—	—	+	+	1,5	+
<i>Clio convexa</i>	—	—	—	+	1	—
<i>Clio cuspidata</i>	—	—	+	+	1,5	+
<i>Clio polita</i>	—	+	+	+	1	+
<i>Clio pyramidata</i> *	—	—	+	—	1	+
<i>Clio recurva</i>	—	—	+	+	5	—
<i>Clio scheelei</i>	—	—	+	—	3	—
<i>Clio sulcata</i>	—	+	—	—	1,5	—
<i>Creseis acicula</i> *	—	—	+	+	1,3,5	+
<i>Creseis chierchiae</i>	—	—	+	+	3,5	+
<i>Creseis</i> sp.*	—	—	+	—		—
<i>Creseis virgula</i>	—	—	+	+	1,3,5	+
<i>Cuvierina columnella</i> *	—	—	+	+	1	+
<i>Diacavolinia angulosa</i> *	—	—	—	+	2	+
<i>Diacavolinia elegans</i>	—	—	+	+	2	—
<i>Diacavolinia longirostris</i>	—	—	—	+	2	—
<i>Diacavolinia mcgowani</i>	—	—	—	+	2	—
<i>Diacavolinia pacifica</i>	—	—	+	+	2	—
<i>Diacavolinia triangulata</i>	—	—	—	+	2	—
<i>Diacavolinia vanutrechtii</i>	—	—	+	+	2	—
<i>Diacria costata</i> *	—	—	—	+	3	—
<i>Diacria danae</i> *	—	—	+	+	3	—
<i>Diacria maculata</i> *	—	—	+	+	4	—
<i>Diacria major</i> *	—	—	+	+	4,5	—
<i>Diacria quadridentata</i>	—	—	—	+	3	+
<i>Diacria rampali</i>	—	—	+	+	4,5	—
<i>Diacria schmidtii</i>	—	—	—	+	3	—
<i>Diacria trispinosa</i>	—	—	+	+	3,4,5	+
<i>Hyalocypris striata</i> *	—	—	+	+	1,3,5	+
<i>Styliola subula</i> *	—	—	+	+	1,3,5	+

shallow water migration by this species might take place to waters above 25 m at night in the Sargasso Sea. These findings agree with our results; at night more than 95% of the individuals were in the upper 90 m and 70% were in the upper 45 m. In both of the preceding studies, the daytime distribution was concentrated in the upper 100 m, while we found low daytime densities between the surface and 300 m.

Wormuth (1981) recorded *Clio pyramidata* down to 1000 m with peak abundances between 240 and 460 m during the day and in the upper 100 m at night. We found that only 4% of the individuals captured at night between the surface and 300 m were present in this depth range during the day, which is consistent with Wormuth's findings from the Sargasso Sea. The results of the two studies differ in that most of the nighttime population in the present study was between 100 and 200 m instead of the upper 100 m as Wormuth reported. The presence of small (1.0–1.1 mm) individuals during the day between 140 and 300 m, a broad size range (to 13.0 mm) at night, and those greater than 6 mm only collected in the upper 90 m at night strongly suggests nocturnal vertical migrations by the adult members of this species.

Limacina lesueuri was reported by Wormuth (1981) to be a nocturnal migrator with 50% of the individuals above 300 m during the day and above 100 m at night. Likewise, Haagensen (1976) reported more than 90% of the individuals above 274 m during the day and above 63 m at night. We found that the total daytime density was only 2% of the total nighttime density above 300 m, implying that most individuals in the population were deeper than the nets fished. At night, >50% of the individuals were in the upper 45 m. Thus, the daytime vertical range off Hawaii may be deeper than in the Sargasso Sea and the Caribbean; however, the nighttime depths of greatest abundance are similar.

Cavolinia inflexa was found by Haagensen (1976) to be a vertical migrator in the Caribbean, with 50% of the population sampled above 261 m during the day and 50% above 50 m at night. Similar results were obtained in this study, as the daytime density above 300 m was 40% of the night density. At night, >50% of the population sampled were found above 90 m.

In the Caribbean, Haagensen (1976) reported migrations of *Cuvierina columnella* from a depth range of 224 to 344 m during the day to above 65 m at night. Similarly, he found 50% of *Hyalocylis striata* above 243 m during the day and above 81 m at night. Wormelle (1962) reported similar findings for *H. striata* in the Florida Current with 50% above 283 m during the day and 84 m at night. In the present study, both species were absent from daytime tows and were limited to the upper 90 m at night, except for one *C. columnella* captured in the 150–200 m interval. During the day, the Bongo nets may have simply missed

individuals that were there or the nets did not fish deep enough to reach the minimum daytime depth of this species. Like the present study, Myers (1967) reported *C. columnella* and *H. striata* off Cape Hatteras to be absent during the day from tows above 150 m, but found both species to be concentrated in the upper 50 m at night.

Three (*Diacria maculata*, *Cavolinia gibbosa*, and *Diacria major*) of the 19 species of euthecosomes identified from Hawaiian waters were captured only at night in extremely low numbers, and comparisons with other studies are not warranted.

CONCLUSIONS

The diel distributions of the 16 most abundant species discussed above are in general agreement with the results obtained for the same species that occur in the North Atlantic Ocean and Caribbean Sea. Six of the species sampled here were permanent residents of the epipelagic zone and showed limited to no diel differences. The majority (10) were either absent or present in low numbers in the upper 300 m during the day and in higher numbers in the upper 140 m at night. If these low densities, or absence during the day, are a result of most of the species' populations residing below 300 m, then these ten species generally dwell in deeper waters off Hawaii than in the North Atlantic and Caribbean.

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Two New Species of *Doriopsilla* from the Tropical Western Atlantic with Remarks on Cariopsillidae Ortea & Espinosa, 2005

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Abstract. Four Caribbean species of *Doriopsilla* are described, including two new species to science. The first detailed anatomical examinations and illustration of living Caribbean animals of *Doriopsilla areolata* and *Doriopsilla nigrolineata* reveals that these are two distinct species. Two undescribed species are differentiated from previously known taxa by a combination of external and anatomical characteristics, including the structure of the digestive and reproductive systems, the presence or absence of black lines and white spots on the dorsum, and the morphology of the dorsal tubercles.

The genus *Cariopsilla* and the family Cariopsillidae are synonymized with *Doriopsilla* and Dendrodorididae respectively, based on the application of modern principles of systematic biology.

INTRODUCTION

Valdés and Ortea (1997) revised the species of the genus *Doriopsilla* in the Atlantic Ocean, regarding only three species as valid. *Doriopsilla areolata* Bergh, 1880, with three subspecies, is distributed through Southern Europe (*D. areolata areolata*), West Africa (*D. areolata albolineata*) and the Caribbean Sea (*D. areolata nigrolineata*). *Doriopsilla pelseneeri* d'Oliveira, 1895 is only present in the Iberian Peninsula, and *Doriopsilla pharpa* Marcus, 1961, is known from the Atlantic coast of North America and the Caribbean Sea. Since then, a third Caribbean species, *Doriopsilla espinosai* Valdés & Ortea, 1998 was described based on material collected from Cuba (Valdés & Ortea, 1998).

More recently, Ortea & Espinosa (2005) erected the new genus *Cariopsilla* Ortea & Espinosa, 2005 and the new family Cariopsillidae Ortea & Espinosa, 2005 for *Doriopsilla pharpa* based on the presence of caryophyllidia-looking tubercles in this species. Valdés et al. (2006) illustrated several additional undescribed species from the Caribbean and brought *Doriopsilla nigrolineata* back to the species level based on consistent morphological differences with *Doriopsilla areolata*.

The present paper deals with the description of two of the new species illustrated by Valdés et al. (2006) and discusses the status of Cariopsillidae based on modern concepts in systematic biology. All specimens are deposited at the Malacology Section of the Natural History Museum of Los Angeles County (LACM).

SPECIES DESCRIPTIONS

Doriopsilla elitae Valdés & Hamann, n. sp.

(Figures 1A–C, 2, 3A)

Doriopsilla sp. 1 – Valdés et al., 2006: 204–205.

Material examined: HOLOTYPE: Vieux Fort, South Point, St. Lucia, 30 m depth, 1 October 1987, 1 specimen 20 mm long, live (LACM 1930). PARATYPE: Petit Nevis, St. Vincent and the Grenadines, 18 m depth, 18 January 1987, 1 specimen 20 mm long, live (LACM 1931). Additional specimens were photographed but are not preserved.

External morphology: Living animals reach up to 20 mm in length. The general color of the living animals is variable from yellow to dark orange (Figure 1A–C). The dorsum is covered with opaque white patches, generally small, and situated on top of many dorsal tubercles. Some of the patches are much larger than the rest, also covering large tubercles situated along the edge of the visceral hump. The rhinophores and gill are the same color as the rest of the body.

The body is flat, oval (Figure 1A–C), stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of low, simple, conical tubercles stiffened with spicules. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 13 lamellae. The

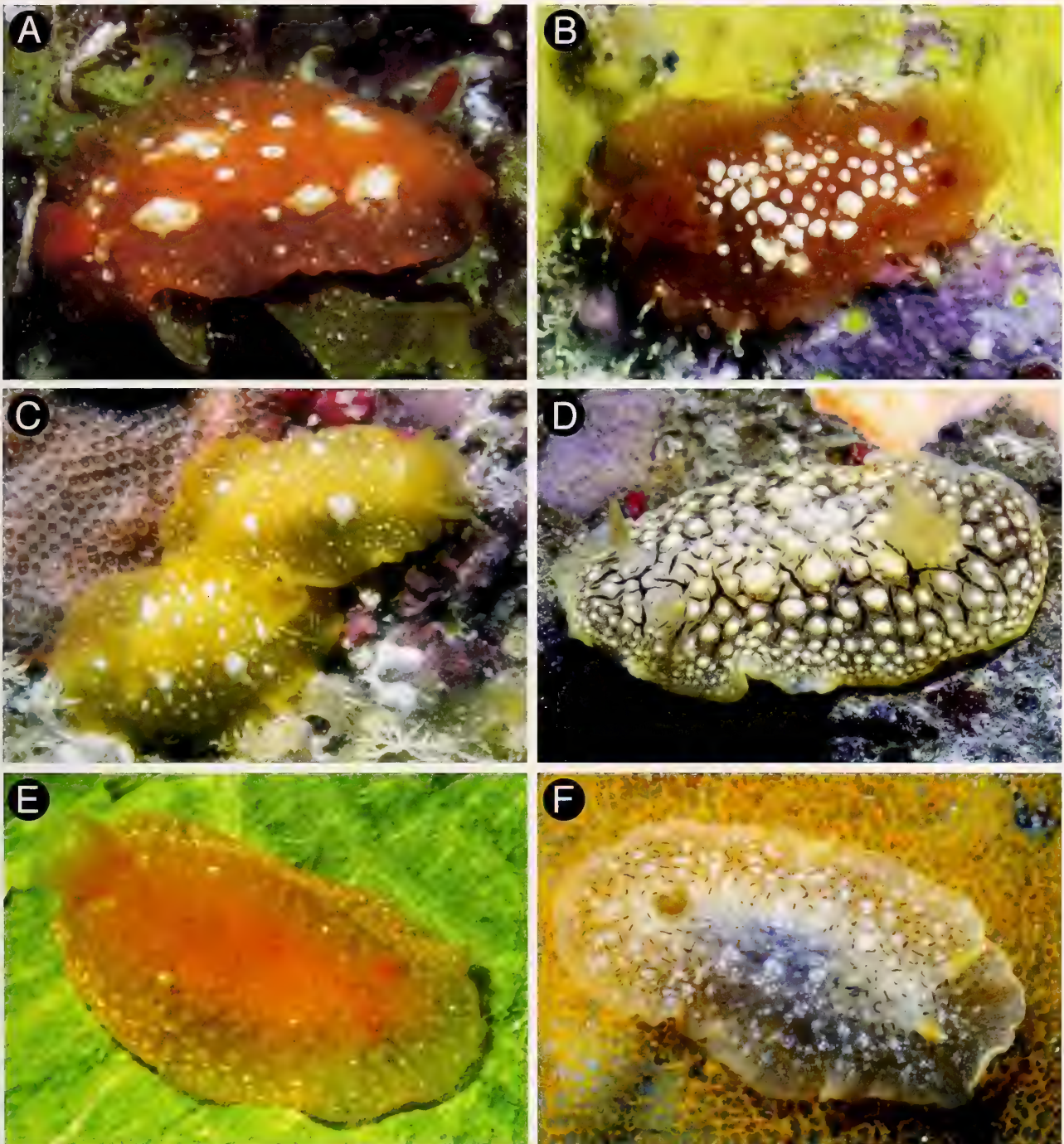


Figure 1. Living animals. A, *Doriopsilla elitae* from St. Vincent, 19 mm long (LACM 1931) – photo Jeff Hamann. B, *Doriopsilla elitae* from Martinique, size unknown – photo Greg Hamann. C, *Doriopsilla elitae* from Aruba, 25 mm long – photo Jeff Hamann. D, *Doriopsilla tishae* from Roatán, Honduras, 49 mm long (LACM 1933) – photo Jeff Hamann. E, *Doriopsilla areolata* from Martinique, 36 mm long (LACM 173780) – photo Jeff Hamann. F, *Doriopsilla nigrolineata* from Guanaja, Honduras, 25 mm long (LACM 173781) – photo photo Jeff Hamann.

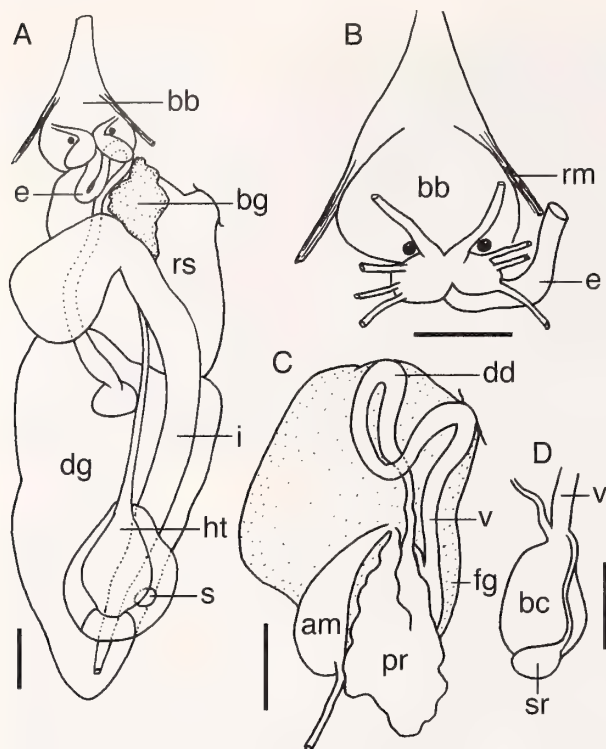


Figure 2. Drawings of the internal anatomy of the paratype of *Doriopsilla elitae* (LACM 1931). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused together with the mouth opening in the center. The anterior border of the foot is slightly concave but not notched.

Anatomy: The buccal bulb is oval (Figure 2A–B), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. The esophagus is very long and convoluted (Figure 2A). Posteriorly, it broadens into a short muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland (Figure 2A).

The ampulla is short and muscular (Figure 2C). It divides into a short oviduct, which enters the female gland, and the prostate. The prostate is broad and flattened. From its distal end, the prostate leads into an elongated and convoluted deferent duct. The penis,

when everted, is very long and contains several rows of penial hooks. The penial hooks are approximately 40 μ m wide at the base and up to 55 μ m in length (Figure 3A). The vagina is long and straight. At its proximal end is a large, thin-walled, oval bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects the bursa copulatrix. From this point also emerges the uterine duct.

The circulatory system consists of a large heart (Figure 2A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Etymology: The species is named after Elita Hamann, middle daughter of Jeff Hamann.

Geographic range: Thus far this species has been collected or photographed in Aruba, St. Vincent and the Grenadines, Grenada, and Martinique.

Remarks: *Doriopsilla elitae* is clearly different from other Atlantic species of the genus. There are no other species with yellow or red background colorations and solid white spots. Species with uniform white, yellow, orange or red colorations include *Doriopsilla areolata* and *Doriopsilla pelseneeri* d'Oliveira, 1895, but the former has a complex pattern of white rings or lines and the latter lacks white pigment except for a single ring around the gill pocket. Anatomically, *Doriopsilla areolata* is clearly different by having a longer, thinner ampulla, a wider prostate, a proportionally larger seminal receptacle, and a much more elongate buccal bulb. *Doriopsilla pelseneeri* lacks any white pigment on the dorsum, except for a white line around the branchial sheath (Valdés & Ortea, 1998). Additionally, *D. pelseneeri* has large, irregular dorsal warts that contrast with the low, simple, conical tubercles of *D. elitae*. For a comparison of the external characteristics of *D. elitae* with other Atlantic species of *Doriopsilla* see Table 1.

Eastern Pacific species of *Doriopsilla* with yellowish to reddish background color and white spots include *Doriopsilla albopunctata* (Cooper, 1863) and *Doriopsilla gemela* Gosliner, Schaefer, & Miller, 1999, both characterized by having very small opaque white spots uniformly distributed over the entire dorsum (see Gosliner, Schaefer, & Miller, 1999), which never form aggregations as in *Doriopsilla elitae*.

Doriopsilla tishae Valdés & Hamann, n. sp.

(Figures 1D, 4–5, 3B)

Doriopsilla sp. 3 – Valdés et al., 2006: 204–205.

Material examined: HOLOTYPE: Coxen's Hole, Roatán, Honduras, 23 December 1991, 1 specimen 49 mm long live (LACM 1932). PARATYPES: Coxen's Hole,

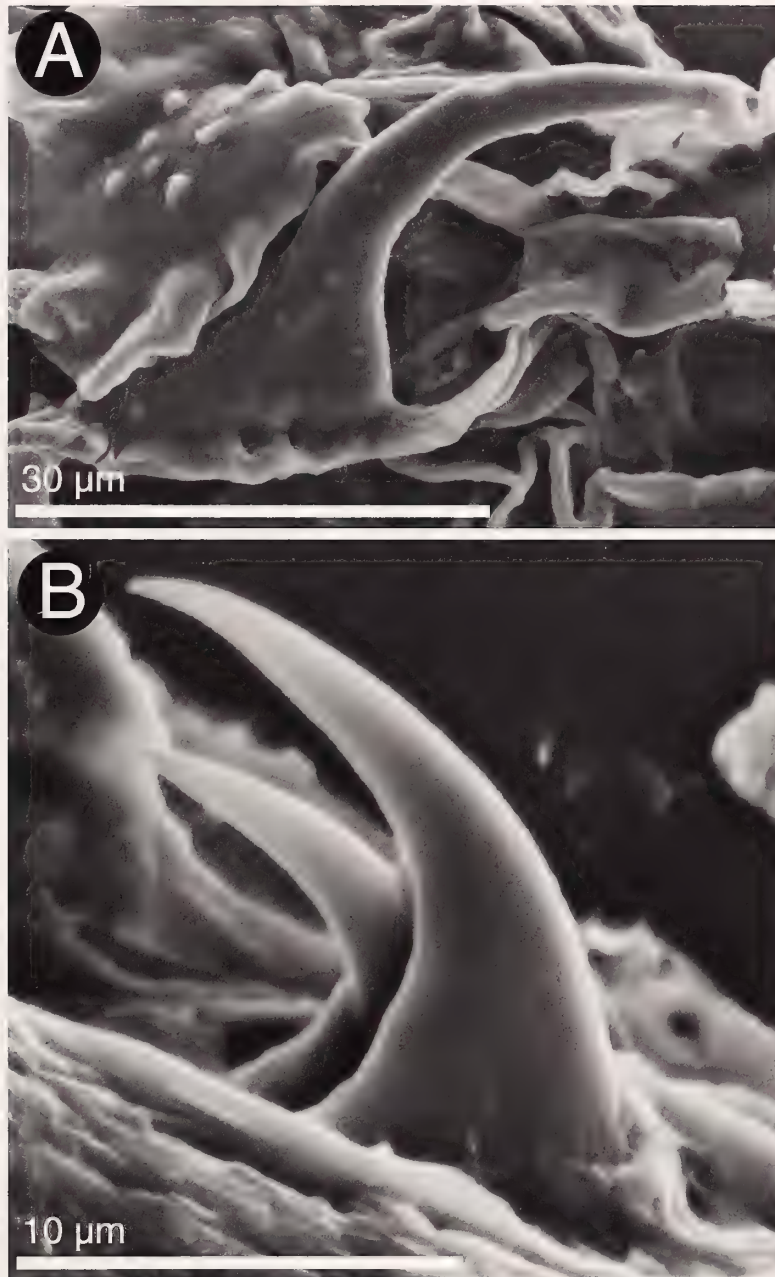


Figure 3. Scanning electron micrographs of penial spines. A, *Doriopsilla elitae* (LACM 1931). B, *Doriopsilla tishae* (LACM 1933).

Roatán, Honduras, 23 December 1991, 5 specimens 49 mm long live (LACM 1933); Soldado Channel, Guanaja, Honduras, 6 August 1991, 30 m depth, 2 specimens 25 mm long live (LACM 1975); Little French Cay, Guanaja, Honduras, 10 August 1991, 1 specimen 27 mm long live (LACM 1976).

External morphology: Living animals reach up to 49 mm in length. The general color of the living animals is translucent yellowish-white (Figure 1D). The

dorsum is covered with a network of anastomosed, irregular, thick black lines running in between the dorsal tubercles. In addition, there are numerous minute opaque white spots concentrated near the edge of the mantle and on top of the dorsal tubercles, giving them the appearance of being completely white. The rhinophores and gill are pale yellow.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of large,

Table 1

Comparative table of the external differences among species of *Doriopsilla* in the Atlantic Ocean.

	Body color	Dorsal tubercles	Geographical range
<i>Doriopsilla areolata</i>	Yellow to pinkish, reddish or pale brown with white rings or lines forming a network, center of the dorsum darker	Low and rounded to conical tubercles, larger in two rows between rhinophores and gills	Eastern Atlantic: from northern Spain to the Cape Verde Islands and Mediterranean Sea. Western Atlantic: Virgin Islands, Puerto Rico, Martinique
<i>Doriopsilla albolineata</i>	Pearl gray with white lines most of which are transverse, brown lines in the mantle margin	Low and simply rounded tubercles, larger in two rows between rhinophores and gills	Atlantic coast of Africa, from Ghana to Angola
<i>Doriopsilla nigrolineata</i>	Translucent yellowish-gray with white rings around tubercles and black lines forming a network	Low and simply rounded tubercles, medial tubercles are higher and larger	Panama, Honduras
<i>Doriopsilla pelseeneeri</i>	White, yellow, orange or red, with a white line around the gill pocket edge	Large irregular warts, larger in the center of the dorsum	Iberian Peninsula
<i>Doriopsilla pharpa</i>	Yellow to orange with numerous dark brown spots on the whole surface of the dorsum	Numerous and minute tubercles, all of them of a similar size	Atlantic coast of the continental USA from Maryland to Florida, and Cuba, Virgin Islands
<i>Doriopsilla espinosai</i>	Translucent white to yellowish with several large opaque white patches, and a number of conspicuous red spots	Numerous low, simple conical tubercles, medial tubercles larger	Cuba, Bahamas
<i>Doriopsilla elitae</i> sp. n.	Yellow to dark orange with opaque white patches situated on top of many dorsal tubercles	Low, simple, conical tubercles	Aruba, St. Vincent and the Grenadines, Grenada, and Martinique
<i>Doriopsilla tishae</i> sp. n.	Translucent yellowish-white with a network of thick black lines and numerous minute opaque white spots near the mantle edge and on the tubercles	Large, semispherical tubercles, larger in the center of the dorsum	Honduras

semispherical tubercles, stiffened with spicules. Tubercles medial on the dorsum are larger, decreasing in size toward the borders of the mantle. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 15 lamellae. The gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is elongate (Figures 4A, 5A), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. At this point two retractor muscles insert onto the posterior of the bulb. The esophagus is very long and convoluted (Figure 5B). Posteriorly, it broadens into a large muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, oval (Figures 4C, 5B). It divides into a short oviduct, which enters the female gland and the prostate. The prostate is broad, flattened. From its distal end, the prostate leads into an elongated deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The penial hooks are approximately 15 μ m wide at the base and

up to 20 μ m in length (Figure 3B). The vagina is very long and convoluted. At its proximal end is a large, thin-walled, spherical bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects the bursa copulatrix. From this point also emerges the uterine duct.

The circulatory system consists in a large heart (Figures 4A, 5A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Etymology: The species is named after Tisha Thiessen, oldest daughter of Jeff Hamann.

Geographic range: Thus far this species is only known from the Bay Islands, Honduras.

Remarks: *Doriopsilla tishae* is most similar to *Doriopsilla nigrolineata* (Figure 1F), originally described from the Caribbean of Panama, due to the presence of dorsal black lines in both species. Differences between these two species include the external coloration and the anatomy. Externally, both species have a pattern of black lines on the dorsum, however, in *D. tishae* the lines are more conspicuous, thicker, longer and consistently anastomosed, whereas in *D. nigrolineata*

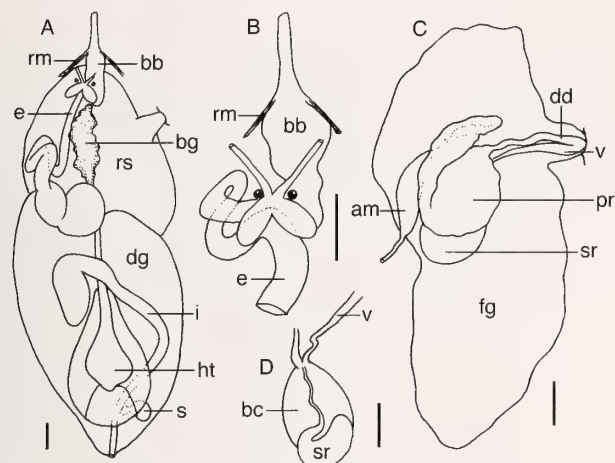


Figure 4. Drawings of the internal anatomy of the paratype of *Doriopsilla tishae* (LACM 1933). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

they are generally shorter, thinner and rarely contact each other (Figure 1F). Additionally, the tubercles of *D. tishae* are much larger than those of *D. nigrolineata*, and are completely covered with opaque white spots, whereas in *D. nigrolineata* the white spots surround smaller and more elongate tubercles. For a comparison of the external characteristics of *D. tishae* with other Atlantic species of *Doriopsilla* see Table 1.

Internally, the structure of the reproductive and digestive system is different. In *D. nigrolineata* the proximal region of the intestine is more inflated and the proximal region of the esophagus is proportionally smaller than those of *D. tishae* (see Figure 6). The buccal bulb of *D. tishae* is elongate, whereas that of *D. nigrolineata* is shorter. The seminal receptacle of *D. nigrolineata* is proportionally larger and joined to the bursa copulatrix by a much shorter duct than in *D. tishae*. No other Atlantic species of *Doriopsilla* have a network of dorsal black lines.

There are no eastern Pacific species of *Doriopsilla* with a color pattern similar to that of *Doriopsilla tishae*.

Doriopsilla areolata Bergh, 1880

(Figures 1E, 7)

Material examined: Anse Noire, North Point, Martinique, 15 July 1987, 30 m depth, 1 specimen 36 mm long

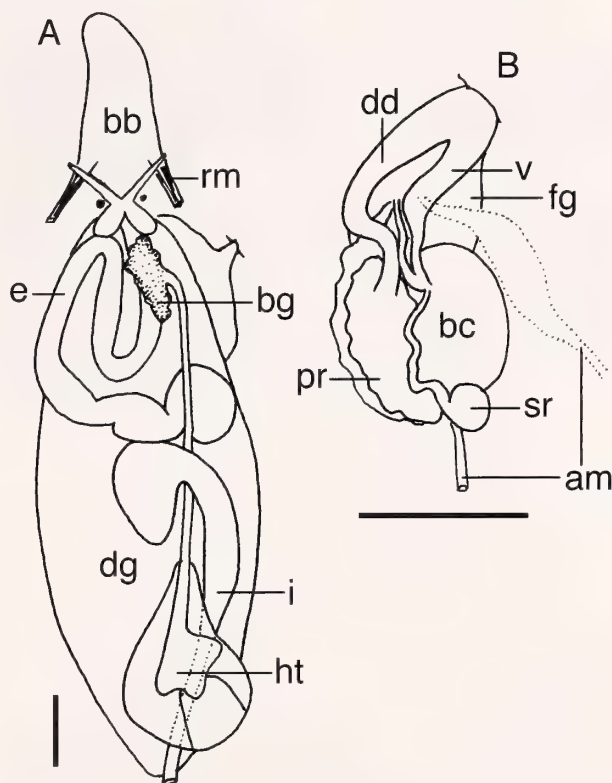


Figure 5. Drawings of the internal anatomy of a paratype of *Doriopsilla tishae* (LACM 1975). A, General view of the anatomy, scale bar = 1 mm. B, Reproductive system, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; sr, seminal receptacle; v, vagina.

live (LACM 173780). Additional specimens were photographed but are not preserved.

External morphology: Living Caribbean animals of this species reach 36 mm in length. The general color of the Caribbean animals varies from yellowish to pinkish or reddish (Figure 1E; Valdés et al., 2006). The dorsum is completely covered with numerous minute opaque bluish-white dots. The largest tubercles, situated on the outer side of the dorsum and inner mantle margin as well as on the branchial sheath, are surrounded by conspicuous white rings composed of accumulations of opaque white dots. The rhinophores and gill are the same color as the dorsum.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of round to conical tubercles, stiffened with spicules. Tubercles on the sides of the dorsum are larger, decreasing in size toward the borders of the mantle and the center of the dorsum. The mantle margin is wide and slightly undulate. The

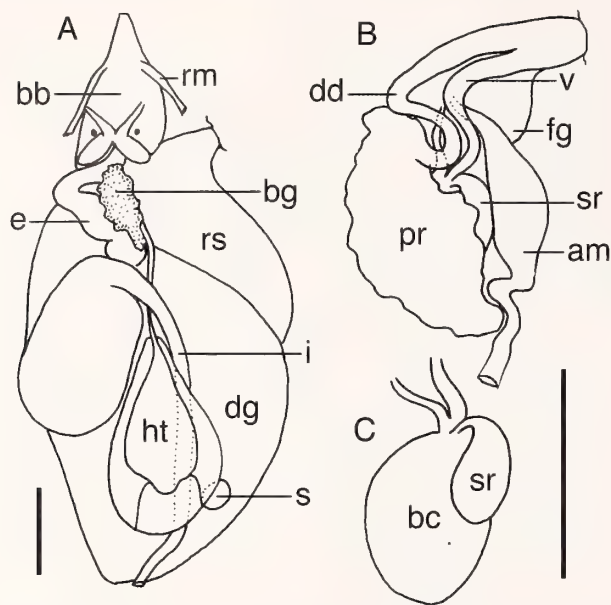


Figure 6. Drawings of the internal anatomy of *Doriopsilla nigrolineata* (LACM 173781). A, General view of the anatomy, scale bar = 1 mm. B, Reproductive system, scale bar as in C. C, Connection of the bursa copulatrix and seminal receptacle, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

rhinophores are perfoliate with up to 12 lamellae. The gill is composed of five tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is very elongate (Figure 7A–B), covered by minute, rather undifferentiated oral glands on its proximal portion. The tubular esophagus leads from the buccal bulb. The esophagus is very long and convoluted (Figure 7B). Posteriorly, it broadens into a small muscular portion. The intestine runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, very elongate (Figure 7D). It divides into a short oviduct, which enters the female gland and the prostate. The prostate is broad, flattened (Figure 7C). From its distal end, the prostate leads into a short deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The vagina is very long and convoluted particularly at its proximal end where it connects to the thin-walled, spherical bursa copulatrix. The seminal receptacle is small, having a long duct that joins the vagina at the point where it connects to the bursa copulatrix. The uterine duct also emerges from this point.

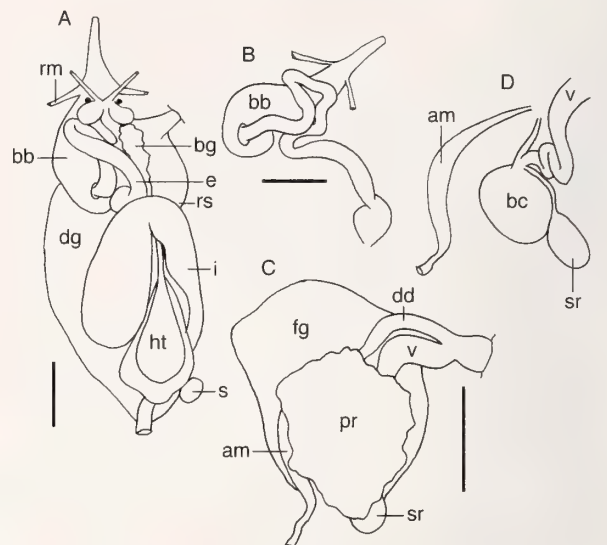


Figure 7. Drawings of the internal anatomy of *Doriopsilla areolata* (LACM 173780). A, General view of the anatomy, scale bar = 1 mm. B, Detail of the anterior portion of the digestive system, scale bar = 1 mm. C, Reproductive system, scale bar = 1 mm. D, Connection of the bursa copulatrix, seminal receptacle, and ampulla, scale bar = 1 mm. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; bg, blood gland; dd, deferent duct; dg, digestive gland; e, esophagus; fg, female gland; ht, heart; i, intestine; pr, prostate; rm, retractor muscle; rs, reproductive system; s, syrinx; sr, seminal receptacle; v, vagina.

Remarks: Eastern Atlantic specimens of this species have been described in detail by Valdés & Ortea (1997). Caribbean specimens are anatomically identical to those from the eastern Atlantic, but they lack the pattern of irregular white lines on the dorsum. Instead they only display the white rings present in juvenile specimens from the eastern Atlantic.

Marcus & Marcus (1962) cited *Doriopsilla areolata* for the Caribbean (St. John, Virgin Islands) based on a single specimen that was preserved before study, therefore the color of living Caribbean animals remained unknown. The anatomical descriptions by Marcus & Marcus (1962) match our observations and the descriptions for eastern Atlantic animals, confirming that they are all members of the same species.

Doriopsilla nigrolineata Meyer, 1977

(Figures 1F, 6)

Material examined: Michael Rock Channel, Guanaja, Honduras, 5 August 1991, 2–3 m depth, 1 specimen 25 mm long, live (LACM 173781). Punta Hospital, Bocas del Toro, Panama, 23 August 2006, 10 m depth, 1 specimen 25 mm long live (LACM 173782).

External morphology: Living animals reach up to

25 mm in length. The general color of the living animals is translucent yellowish-gray (Figure 1F). The viscera is visible through the skin as a dark gray area. The dorsum is covered with a series of thin, irregular black lines running in between the dorsal tubercles and almost never contacting each other. In some specimens the lines may be longer than in others. In addition, there are numerous minute opaque white spots all over the dorsum, forming rings around the dorsal tubercles but never on the tubercles themselves. The rhinophores and gill are pale yellow. The rhinophores have white apices.

The body is oval, low, stiffened by a subepidermal network of strong spicules over the entire body surface. The dorsum is covered by a number of round tubercles, stiffened with spicules. Medial tubercles on the dorsum are higher and larger, decreasing in length and size toward the borders of the mantle. The mantle margin is wide and slightly undulate. The rhinophores are perfoliate with up to 12 lamellae. The gill is composed of four tripinnate leaves. The anus is eccentric to the left.

The oral tentacles are fused and grooved laterally. The anterior border of the foot is notched.

Anatomy: The buccal bulb is short and wide (Figure 6A), covered by minute, rather undifferentiated oral glands. The tubular esophagus leads from the buccal bulb. The esophagus is short and convoluted. Posteriorly, it broadens into a muscular portion. The intestine is greatly expanded proximally, runs posteriorly in the usual position and lacks any pyloric gland.

The ampulla is simple, elongate (Figure 6B) and enters the female gland near the opening of the prostate. The prostate is broad and flattened. From its distal end, the prostate leads into a relatively short deferent duct. The penis, when everted, is very long and contains several rows of penial hooks. The vagina is short and convoluted. At its proximal end is an oval, thin-walled bursa copulatrix. The seminal receptacle is small, having a very short duct that joins the vagina at the point where it connects the bursa copulatrix (Figure 6C). From this point also emerges the uterine duct.

The circulatory system consists in a large heart (Figure 6A), joined by the aorta with a flattened blood gland, situated behind the central nervous system.

Geographic range: Originally described from Panama, this species has been subsequently collected and photographed from Honduras.

Remarks: The original description of this species (Meyer, 1977) was based on external characteristics but did not include anatomical examinations. The redescription by Valdés & Ortea (1997) was a re-examination of the external morphology of the

holotype and produced no new information. The present paper provides the first anatomical examination of this species, which clearly differs from *Doriopsilla areolata* in several regards. Differences include the length of the buccal bulb, which is several times longer in *D. areolata* than in *Doriopsilla nigrolineata*. Also the structure of the reproductive system is different in these two species, with a larger seminal receptacle in *D. nigrolineata* connected to the bursa copulatrix by a much shorter duct. Finally, the ampulla is proportionally longer in *D. areolata*. Externally these two species are readily distinguishable by the presence of irregular black lines in *D. nigrolineata* that are absent in *D. areolata*.

DISCUSSION

Cariopsillidae Ortea & Espinosa, 2005, type genus *Cariopsilla* Ortea & Espinosa, 2005, was described based on the species *Doriopsilla pharpa* Marcus, 1961, which has dorsal tubercles superficially similar to the caryophyllidia present in other dorid nudibranchs. Ortea & Espinosa (2005) indicated that this new taxon is proposed to rationalize the systematics of radula-less dorids, independently from phylogenetic studies that produce erroneous results due to the incorrect use of characters. More specifically, Ortea & Espinosa (2005) criticized the phylogenetic analysis conducted by Valdés & Gosliner (1999) because of the exclusion of characters referring to the caryophyllidia-like tubercles of *D. pharpa*.

According to the only available phylogenetic hypothesis including *D. pharpa* (Valdés & Gosliner, 1999), this species is nested in the *Doriopsilla* clade, so the introduction of a new genus and a new family for this species would render both *Doriopsilla* and Dendrodorididae as paraphyletic. Ortea & Espinosa (2005) did not provide arguments to support the evolutionary distinctiveness of *D. pharpa* or a phylogenetic hypothesis to support their alternative grouping. For all these reasons, and until new evidence becomes available, we regard Cariopsillidae as a junior synonym of Dendrodorididae and *Cariopsilla* as a junior synonym of *Doriopsilla*.

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Lindsey Groves (LACM) curated the specimens collected and critically reviewed the manuscript. An anonymous reviewer and Elita Hamann made constructive comments on the manuscript. Elita Hamann also reviewed the manuscript for grammar and consistency.

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Dendropoma mejillonensis sp. nov., a New Species of Vermetid (Caenogastropoda) from Northern Chile

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Abstract. *Dendropoma mejillonensis* sp. nov. is described based on morphology for the first time. This vermetid gastropod inhabits the rocky subtidal zone of Peninsula Mejillones in northern Chile. In July 2006, specimens were collected by SCUBA divers from the rocky “Anemones Wall” (23°28′17.30″S, 70°37′13.80″W) at 17 m depth. The morphology of *D. mejillonensis* is distinguished from that of other members of the family by its pointed lip on the external border of the protoconch and the two white bands on the head tentacles. This extends the geographical range of the genus *Dendropoma* into the Southeastern Pacific. The present species *D. mejillonensis* is the only known vermetid gastropod able to thrive under the cold upwelling conditions of the Humboldt Current ecosystem off northern Chile.

INTRODUCTION

Marine gastropods of the family Vermetidae are sessile organisms with an irregular, uncoiled shell providing a three-dimensional biogenic habitat for associated species. Their distribution is restricted to tropical and subtropical latitudes (Mexico, California and West Africa) as well as to locations in the warm Mediterranean Sea (Keen, 1961, 1971; Schiaparelli et al., 2003). Habitats are rocky intertidal and subtidal zones with warm and oxygenated waters (Keen, 1961; Calvo et al., 1998). Due to the irregular tube form, taxonomic identification has commonly been confused with *Vermicularia* (Turritellidae) (Bieler, 1996) and Serpulid polychaetes (Keen, 1961, 1971) resulting in a confused taxonomic status. The morphological characters deemed useful for taxonomic identification have changed over time (Bieler, 1995; Schiaparelli & Métivier, 2000). A genetic study further concluded that disjunct populations of *Dendropoma* species are close phylogenetic relatives (Rawlings et al., 2001), thus suggesting that taxonomic determination should be approached carefully.

The genus *Dendropoma* (Mörch, 1861) was reviewed by Keen (1961) on the basis of 10 species distributed among tropical and subtropical locations. Distinctive morphological characteristics for this genus are planorboid early whorls that become more loosely coiled in later stages; and the sculpture of lamellar growth-striations that may or may not be intersected by longitudinal lines, sinuous and rising toward a crest near the outer edge of the whorl in most species. The

operculum is well developed and equal in diameter to the aperture. At present, the genus *Dendropoma* covers intertidal and sublittoral species and can be gregarious or solitary. So far, the most comprehensive information about *Dendropoma* spp. taxonomy is provided by Hadfield et al. (1972) for specimens found off Hawaii.

Information on the distribution of vermetids off continental Chile and its offshore islands is scarce and the taxonomic status is still uncertain (Rehder, 1980; Ramírez & Osorio, 2000; R. Bieler pers. comm.). In fact, extensive reviews of gastropod taxonomy and studies of invertebrate biogeographic patterns available from this coast do not mention the family in the region (Marincovich, 1973; Guzmán et al., 1998; Brattström & Johanssen, 1983; Valdovinos, 1999; Lancellotti & Vásquez, 2000). Anecdotally, vermetids have been observed associated with holdfasts of the kelp *Lessonia trabeculata* Villouta & Santelices, 1986 off central Chile (Vásquez & Vega, 2004). With the exception of the latter observation, there is no published evidence from the Chilean coast. Nonetheless, *Dendropoma platypus* Mörch, 1861; *Dendropoma* spp. and *Serpulorbis* Sassi, 1827 have been recorded from Easter Island (Rehder, 1980; Ramírez, 1987; Valdovinos, 1999) and *Serpulorbis* sp. was also observed at Robinson Crusoe Island (Juan Fernández archipelago) (Ramírez & Osorio, 2000), both insular Chilean locations.

Northern Chile forms part of the Humboldt Current upwelling ecosystem, which is characterized by year-round high levels of primary production due to wind-driven cold upwelling water, which returns nutrients to the euphotic zone (Barber & Smith, 1981). There is a shallow oxygen minimum zone (OMZ) and only the upper 40 m are well oxygenated (Arntz et al., 2006).

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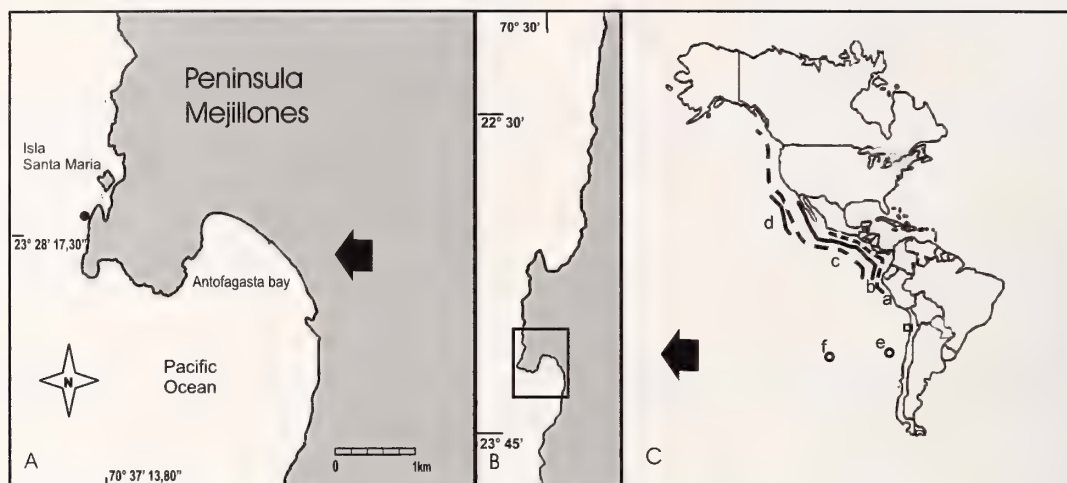


Figure 1. A. Sampling location "Anemones Wall" ($23^{\circ}28'17.30''\text{S}$, $70^{\circ}37'13.80''\text{W}$) opposite the southeastern side of Isla Santa Maria. B. Peninsula Mejillones. C. Distributional range of related vermetid species (a) *Petalonchus innumabilis* (b) *Serpulorbis squamigerus* (c) *Vermetus compta* (d) *Dendropoma rastrum* (e) *Serpulorbis* sp. (f) *Dendropoma platypus*.

This habitat is very different from that of warm-water subtropical and tropical vermetid species. In this study *Dendropoma mejillonensis* sp. nov. is described from Peninsula Mejillones, a location within this particular upwelling system. A detailed morphological characterization is provided.

MATERIAL AND METHODS

Individuals of *Dendropoma mejillonensis* sp. nov. colonizing a vertical rock wall in the subtidal zone (17 m depth) of Peninsula Mejillones ($23^{\circ}28'17.30''\text{S}$, $70^{\circ}37'13.80''\text{W}$) were photographed and collected by SCUBA divers on July 11th, 2006 (Figure 1A, B). Several vermetid clusters were scratched from the rock with a knife and maintained in the laboratory for observations. Measurements were taken with a digital caliper or by using calibrated eyepieces on a dissecting microscope. Photographs were taken with a Canon Power Shot S50 camera connected to a binocular microscope Olympus SZ61. Animals were anesthetized by adding methanol drops in the small examination containers before sacrificing. Soft bodies were removed from the shell after cracking with a small clamp. Gross anatomy of the soft parts was studied under a dissection microscope. Air-dried shells, radula, protoconch and opercula were observed and photographed, using the scanning electron microscope JEOL, model JSM- 6360LV.

Diagnosis

Genus *Dendropoma* Mörch 1861

Solitary to colonial forms, corroding a trench in the substrate, in which the lower part of each volution is

embedded; coiling planorboid in early whorls, becoming looser in later whorls, with tendency toward right-angle turns. The color of the adult is mostly white, intermittently stained with dark brown, especially within. The sculpture of lamellar growth-striations, that may or may not be intersected by longitudinal lines, is sinuous and rises toward a crest near the outer edge of the whorl in most species. Two nuclear whorls are dark brown in color, inflated, smooth to malleated or axially ribbed, and the aperture lip is pointed or claw-like in some species. The operculum is well developed, as large as the aperture, its inner surface having a distinct central attachment scar that is somewhat button-like, and its exterior composed of chitinous plates in a spiral arrangement, either compactly welded to form a smooth surface or variously agglutinated with foreign materials.

Dendropoma mejillonensis sp. nov.

Type locality: Live-taken syntypes collected from a large aggregation colonizing Anemones wall at 17 m depth, Peninsula Mejillones, northern Chile ($23^{\circ}28'17.30''\text{S}$, $70^{\circ}37'13.80''\text{W}$) were deposited in the Field Museum of Natural History, Chicago, Illinois, U.S.A. (FMNH N°-312172 and N°-312173). Additional samples were deposited in the Museo Nacional de Historia Natural de Santiago de Chile (paratype MNHNCL N°-5159 and syntypes MNHNCL N°-5160, 5161, 5162).

Teloconch (Figure 2a, b): The tubes form continuous and compact colonies, which are grey to faintly green in the field, but white after cleaning. *In situ*, the tubes are slightly nested in the rocky substrate. The attached part of the tube appears eroded, and thus is thinner (Figure 2d). The aperture is circular and its mean

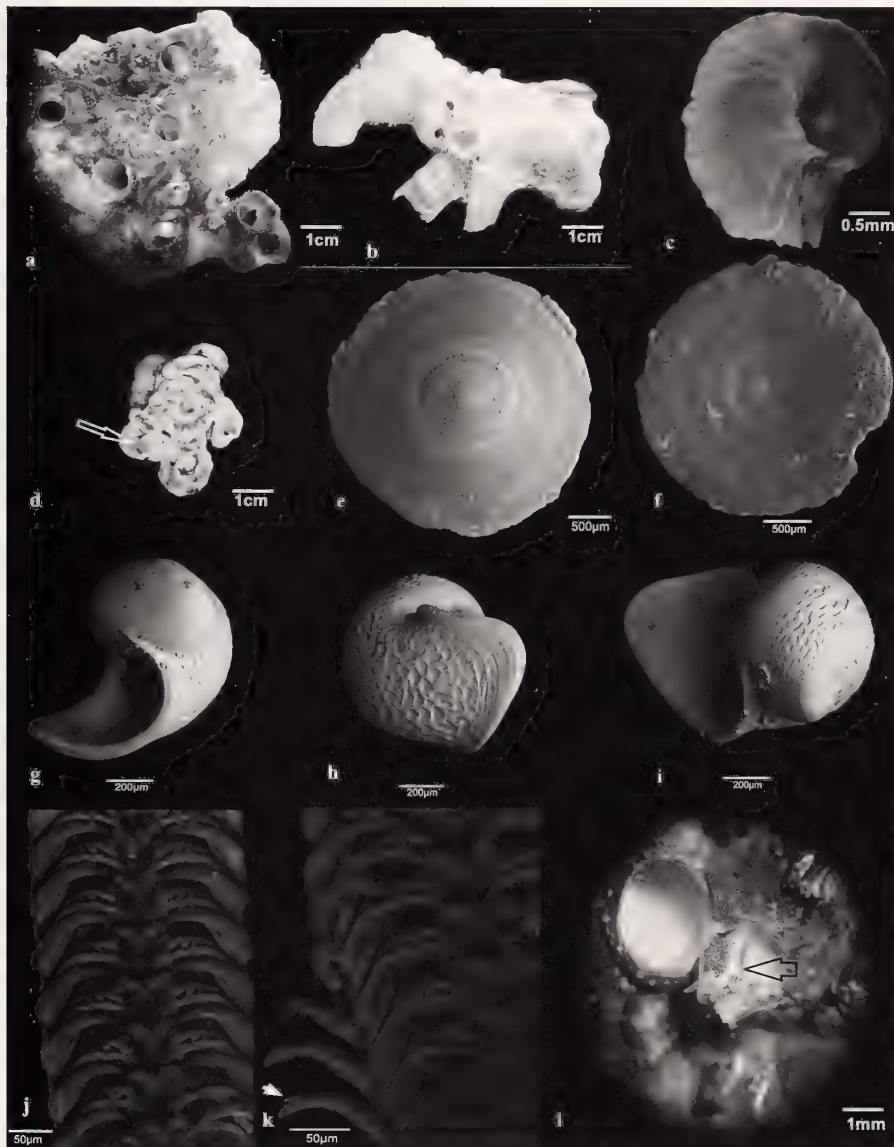


Figure 2. *Dendropoma mejillonensis* sp. nov. (a) Mass of living adult tubes. (b) Lateral view (c) Teleconch of juvenile showing concentric growth striations. (d) Smooth eroded part showed from the attached part of the tubes. (e) Operculum dorsal view. (f) Operculum ventral view. (g) Protoconch aperture. (h) Protoconch; detail of the sculpture and pointed lip-like external border. (i) Protoconch in ventral position, the earliest whorl is noted. (j) Radula displacement. (k) Detail of the cusp on the marginal teeth. (l) View of the animal head, the arrow points to the distinctive white mark.

diameter in adults is 4.29 mm ($SD = 0.37$; $n = 16$). The tube exhibits sinuous growth lines and the sculpture of lamellar growth-striations is not intersected by longitudinal lines (Figure 2c). The periostracum is white and the intermediate layer slightly cream. Observing from a cross-longitudinal section, three layers of the conch are present. The interior part is cream porcelain, darker towards the interior tube. Very soft longitudinal lines are only observed under magnification. There is no internal shell lamellar structure. The proximal part of the tube slightly tends to vertically rise from the rest of

the mat. The coiling pattern is variable. Early whorls are like Planorbidae, coiling counterclockwise, followed by a very loose coiling or irregular pattern. The shell of the juvenile is white and translucent with clear axial ribs (Figure 2c).

Operculum (Figure 2e, f): The form is circular and concave, slightly flattened and reddish in the center, brown-orange to colorless towards the external border. The diameter is 2.7 mm ($SD = 0.2$; $n = 10$) in adult specimens and about 1/5 of the length of the relaxed

pedal disk diameter. The operculum is composed of concentric layers of chitinous material with visible concentric irregular lines, notably in juveniles. The small mamilla is inserted in the pedal surface. Almost 90% of the studied opercula were fouled with bryozoans.

Protoconch (Figure 2g, h, i): Globular, brown or colorless, white towards the earliest whorl. The shell shows 1 to 1.5 nuclear whorls, ornamented with longitudinal grooves. The grooves show no evident axial pattern, are variable in size and present a slightly rectangular or triangular shape with no marks at the corners. The external border presents a pointed lip shape and growths striations are present. At hatching, shell length (the distance from the external lip border to the opposite whorl margin) is 0.77 mm (SD = 0.07; n = 10).

Radula (Figure 2j, k): Taenioglossan type, similar to the description of other vermetids (i.e., *Vermetus triquetrus* Bivona-Bernardi, 1832 and *Thylaeodus rugulosus* Monterosato, 1878; Bieler, 1995), transparent, consisting on average of 39.8 (SD = 6.06) rows of teeth (counts and measurements based on adult animals of 4 mm shell aperture, n = 10, no differences between sexes were noted). Total length of radular ribbon is 2.35 mm (SD = 0.34) and 0.196 mm width (SD = 0.011, mid ribbon). A trapezoidal rachidian tooth with a strong main cusp and 4–5 flanking cups on either side (diminishing toward margin), basal denticles strongly developed. Lateral tooth cusp arrangement of triangular cutting shape, as in the central tooth, with two flanking cusps on either side. The inner marginal tooth is slender with a strong main cusp and the inner marginal with one flanking cusp on inside and two on outside. The outer marginal teeth present a single flanking cusp smooth on outside. Radular formula: 2+1+R+1+2.

Animal: Removed from the shell the body is short and narrowest towards the terminal part, which is slightly coiled. The average length of relaxed large adult specimens is 18.66 mm (SD = 1.68; n = 10). The head is mainly light grey or reddish with black, white and yellow specks. The posterior part is reddish or dark brown in color. Two white bands on the head tentacles are distinctive appearing as a white eyebrow (Figure 2l). The head tentacles are brown or light grey in color with black and yellow dots, no distinctive marks at the tips are visible. The pedal tentacles are light grey with yellow specks. In both sexes the light orange/melon mantle is entire and is characterized by a light brown border. The foot is a similar color to the mantle; however it has a white band around the operculum insertion. The gill filaments are about 1/3 of the size of the mantle and slightly triangular in shape. The

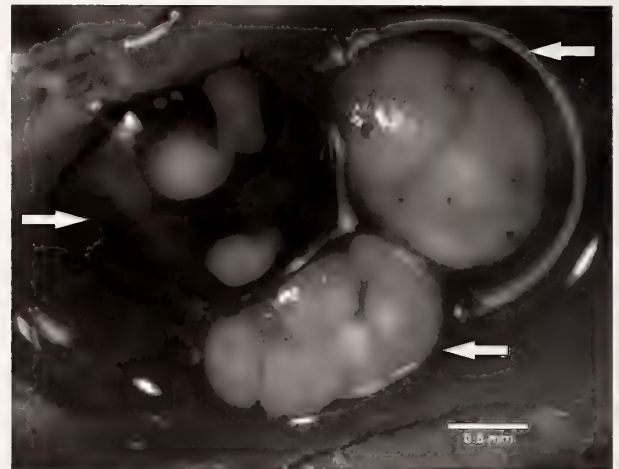


Figure 3. Capsules of *Dendropoma mejillonensis* sp. nov. containing juveniles (arrow left side) and nurse yolk (arrows right side).

columellar muscle appears as a white triangular narrow strip, enabling the animal to retreat deeply into its shell. Female's broods comprise three to four egg capsules, which are ovoid and the membrane is translucent. Each capsule contains between three to ten juveniles. Early capsules contain nurse yolk (Figure 3). Feeding is carried out by mucous threads.

Habitat: The specimens were attached to a vertical rock wall, which extends from the shallow subtidal down to 50 m depth. In the field, colonies showed a light grey to white color and were commonly fouled by calcareous algae causing a red/purple coloration. The surrounding benthic community is dominated by the kelp *Lessonia trabeculata* from 13 m depth down to 25 m. Below 25 m, kelp abundance is substantially reduced and relatively small epibenthic taxa such as calcareous algae (*Lythothamnium* sp. and *Lithophyllum* sp.), red algae (*Rhodomenia corallina* Bory de Saint Vincent & Greville), bryozoans (*Membranipora isabelleana* D'Orbigny, 1847 and *Lagenicella variabilis* Moyano, 1991), and Porifera cover the substrate. *Dendropoma mejillonensis* sp. nov. colonies were observed between 15 and 25 m.

Etymology: The species is named *Dendropoma mejillonensis* in reference to the discovery location Peninsula Mejillon.

DISCUSSION

Taxonomic remarks

The morphological classification of the species to the *Dendropoma* genus was carried out following Keen (1961). *Dendropoma mejillonensis* sp. nov. shows similarities to *Dendropoma gregaria* Hadfield & Kay,

1972 (Hadfield et al., 1972) from Hawaii, sharing the circular pattern in the operculum and dense white pigmentation around the eyes. The most noteworthy difference is in the protoconch sculpture, while *D. gregaria* has light axial ribs crossed by finer spiral striations, *D. mejillonensis* shows soft grooves without evident design shape and pattern.

Distributional Remarks

As already mentioned, the presence of vermetid gastropods is limited along the Pacific coast of South America. Alamo & Valdivieso (1997) reported *Petalconchus innumerabilis* Pilsbry & Olsson 1935 from Mazatlán (Mexico) to Bocapan and Huacho (Peru), *Serpulorbis squamigerus* Carpenter, 1857 from San Diego (California) to Paita (Peru) and *Vermetus compta* Carpenter, 1857 from British Columbia (Canada) to Paita. Keen (1971) recorded *Dendropoma lituella* Mörch, 1861 and *Dendropoma rastrum* Mörch, 1861 from the northern part of the Eastern Pacific; both were found from southern California to the southern Gulf of California at La Paz, Baja California (see also Figure 1c).

The presence of *Dendropoma mejillonensis* in the rocky subtidal zone of Peninsula Mejillones clearly extends the geographic range of the family into the Southeastern Pacific, almost 2000 km southwards. According to the literature the closest distribution limit of vermetids is Huacho (11°6'56.21"S, 77°37'9.46"W) (Alamo & Valdivieso, 1997). Easter Island and Juan Fernández may be source locations if *Dendropoma* sp. is *D. mejillonensis*, in this case the range would be extended from insular to continental Chile. However, it is not possible to define the biogeography of this species, as we did not sample south or north of the type locality.

Our record provides evidence that *D. mejillonensis* is able to thrive under cold upwelling conditions. The observed recruitment at Anemones Wall (A. Pacheco unpublished data) indicates that this species has the capacity to adapt to cold upwelling conditions. The species' distribution may be limited by the presence of a short larval stage. As in the case of many other vermetids (Keen, 1961; Hadfield et al., 1972; Calvo et al., 1998), larvae of *D. mejillonensis* leave the female mantle cavity well developed and crawl around for less than one hour before cementing themselves to the substrate. The recent discovery from Peninsula Mejillones suggests that several unexplored areas with unreported species may still exist along the northern Chilean coastline, particularly in zones difficult to reach (Camus, 2001). Furthermore, distributions of rafting species (a dispersal mechanism suggested for vermetids (Bieler, 1995)) may extend quickly with an increasing amount of anthropogenic floating material,

facilitating the supply of sessile species to new regions (Thiel & Haye, 2006). A genetic study is necessary to reveal linkages between *D. mejillonensis* and other vermetids.

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New Genera and Species of Peristerniinae (Gastropoda: Fascioliidae) from the Caribbean Region, with Comments on the Fascioliid Fauna of Bermuda

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Abstract. Three new genera of *Latirus*-like gastropods from the western Atlantic are described and distinguished from *Hemipolygona*, *Polygona*, and *Pustulaturus*, all peristerniine genera with sympatric species in the region, and from *Fusolaturus* of the Indo-west Pacific. The new genera are: *Lamellilaturus*, type species *Fusus ceramidus* Dall, 1889a, formerly classified in *Fusinus*, Recent, southern Caribbean Sea; *Lightbournus*, type species *L. russjenseni* sp. nov., Recent, Bermuda; and *Bullockus*, type species *B. guesti*, Recent, Bermuda; *Bullockus pseudovarai* sp. nov., Recent, eastern Bahamas, is also described. Other species reclassified in *Bullockus* are *Latirus* (*Hemipolygona*) *mcmurrayi* Clench and Aguayo, 1941, from northern Cuba and the Bahamas; *Latirus* (*Latirus*) *varai* Bullock, 1970, from eastern Cuba; and *Hemipolygona honkeri* Snyder, 2006, from the Bahamas and southwestern Caribbean Sea. Species of *Bullockus* generally live in upper slope depths (183–550 m), although one occurrence of *B. guesti* from 51 m is known. Pleistocene and Recent records of *Latirus brevicaudatus* (Reeve, 1847) at Bermuda are disproved; Pleistocene occurrence of *Leucozonia nassa* (Gmelin, 1791) at Bermuda is confirmed; and Pleistocene and Recent records of *Fasciolaria* spp. at Bermuda remain unconfirmed.

INTRODUCTION

Western Atlantic species of the fascioliid subfamily Peristerniinae customarily have been classified in only two genera, *Latirus* Montfort, 1810, and *Leucozonia* Gray, 1847 (e.g., Bullock, 1974; Vermeij and Snyder, 2002; Mallard and Robin, 2005). However, recent studies of peristerniine taxa world-wide have reclassified many species formerly in *Latirus* to other genera such as *Benimakia* Habe, 1958 (Vermeij and Snyder, 2003) and *Fusolaturus* Kuroda and Habe, 1971 (Snyder and Callomon, 2005; Snyder and Bouchet, 2006). Vermeij and Snyder (2006) further restricted *Latirus* to a relatively few Indo-west Pacific species, raised *Polygona* Schumacher, 1817 and *Hemipolygona* Rovereto, 1899, both formerly considered subgenera of *Latirus*, to full generic rank, and introduced the new generic names *Pustulaturus* and *Turritaturus* to accommodate other species formerly classified in *Latirus*. These studies prompted reassignment of nearly all western Atlantic species formerly assigned to *Latirus* to *Polygona*, *Hemipolygona*, *Benimakia*, or *Pustulaturus*, most by Vermeij and Snyder (2006).

One western Atlantic species whose classification has

not been addressed in those studies is *Fusus ceramidus* Dall, 1889a. This species has usually been classified in the genus *Fusinus* Rafinesque, 1815 (e.g., Hadorn and Rogers, 2000), but Sunderland and Sunderland (1995) proposed that the shell seemed more like that of *Latirus*, and Snyder (2003) noted that a review of western Atlantic *Latirus* by Bullock (1968; unpublished M.Sci. thesis) had indeed placed the species in that genus. Bullock's account confirmed that the species is peristerniine and, by criteria in use at that time, was appropriately placed in *Latirus*, but it is excluded from that genus by contemporary criteria.

To ascertain a proper generic assignment for "*Latirus*" *ceramidus*, we examined shells from the type locality, Barbados, and from another reported population at Bermuda. This examination convinced us that no generic name currently in use is appropriate for this species, so we introduce a new generic name for it. "*Latirus*" *ceramidus* is redescribed, and evidence pertinent to its generic distinctiveness is discussed. The Bermuda material was found not to be "*L.*" *ceramidus* but rather to consist of two previously undescribed species which we also describe. These species, both apparently endemic to Bermuda, are

designated as type species of two other new genera, one containing several additional Caribbean species, including another newly described here. The other new genus is monotypic. It is possible that these genera are deep-water derivatives of *Hemipolygona*.

METHODS

Specimens were examined from several institutional and private collections, identified by prefixes of catalogue numbers or collectors' initials (see Abbreviations). Shells were measured to the nearest 0.1 mm using vernier calipers. Unless otherwise stated, reported sizes are shell height (greatest length).

Abbreviations

- ANSP – Academy of Natural Sciences of Philadelphia, PA.
 BMSM – Bailey-Matthews Shell Museum, Sanibel, FL.
 DMNH – Delaware Museum of Natural History, Wilmington, DE.
 FLMNH – Florida Museum of Natural History, Gainesville, FL.
 HGL – Collection of Harry G. Lee, Jacksonville, FL.
 KLS – Collection of Kevan & Linda Sunderland, Sunrise, FL.
 MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA.
 RH – Collection of Roland Hadorn, Lyss, Switzerland.
 Sh – empty (dead) shell.
 USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 WGL – Collection of William G. Lyons, St. Petersburg, FL.

SYSTEMATICS

Class Gastropoda Cuvier, 1795
 Family Fascioliariidae J. E. Gray, 1853
 Subfamily Peristerniinae Tryon, 1880

Lamellilaturus gen. nov.

Type species: *Fusus ceramidus* Dall, 1889a, Recent, Barbados, designated herein.

Diagnosis: Peristerniine gastropods with fusiform shells of small to medium size (adult lengths to 51.0 mm); whorls sculpted with moderate to strong axial ribs and less prominent spiral cords; sutures distinct, bordered anteriorly by prominent, dense band of lamellae; siphonal canals relatively short, slender, canted to left; aperture ovate, constricted anteriorly and posteriorly, with parietal shield bearing very weak, oblique columellar plicae and outer lip bearing internal lirae that are entire posteriorly but interrupted as beaded

dots and dashes (*sensu* Vermeij and Snyder, 2006) anteriorly on mature specimens; radula of *Latirus*-type (see Cernohorsky, 1972:156–159 for examples of *Latirus*-type and *Peristernia*-type radulae).

Etymology: *Lamellilaturus*, masculine, is a compound word formed of *lamella*, Latin, the diminutive of *lamina*, or plate, in reference to the prominent subsutural lamellae of the shells, and the stem name *Latirus*, to acknowledge the place of the genus among the “*Latirus*-like” taxa.

Remarks: *Lamellilaturus* is distinguished from *Fusinus*, where the type species was previously placed, by its peristerniine rather than fusinine radula (see Figure 3) and by having faint but definite oblique columellar folds (noted by Bullock (1968: 60)); shells of *Fusinus* lack columellar folds. Its relatively light-weight shells bearing conspicuous subsutural axial lamellae and faint oblique columellar plicae distinguish *Lamellilaturus* from other *Latirus*-like genera, most of which have heavier shells with well-developed, near-perpendicular columellar plicae. Shells of some species of the Indo-west Pacific genus *Fusolatirus* resemble those of *Lamellilaturus* but differ by having a *Peristernia*-like radula (see Snyder and Bouchet (2006: fig. 3k) for the radula of *Fusolatirus*).

Abbott (1974) incorrectly classified *Fusinus ceramidus*, the type species of *Lamellilaturus*, in the subgenus *Barbarofusus* Grabau and Shimer, 1909, which has been considered a subgenus or synonym of *Fusinus* or of *Heilprinia* Grabau, 1904. Shells of *Barbarofusus* lack columellar folds and subsutural lamellae, and their protoconchs are prominently ribbed on all whorls, whereas the protoconch of *F. ceramidus* is essentially smooth except for a few fine riblets near the junction with the teleoconch. Bullock (1968) and Sunderland and Sunderland (1995) proposed that *Fusus ceramidus* is more appropriately classified in *Latirus*, and Bullock (1968) proposed a manuscript name for a subgenus of *Latirus* with *ceramidus* as its type species. We chose not to validate that name because Bullock intended it collectively to represent several species that we do not believe represent a natural species-grouping.

Lamellilaturus ceramidus (Dall, 1889a)

Figures 1–2

Fusus ceramidus Dall, 1889a: 14, 171; Dall, 1890: 318, 359, pl. 6, fig. 6; Grabau, 1904: 74, 75; Lewis, 1965: 1067; Boss *et al.*, 1968: 70; Bullock, 1968: 59, 106, 107, pl. 8, fig. 7; Hadorn & Rogers, 2000: 14; Snyder, 2003: 64.

Latirus ceramidus: Bullock, 1968: 59–61, 96, 106, pl. 3, figs. 5, 8.

Fusinus ceramidus: Abbott, 1974: 230, 231, text-fig. 2530; Lyons, 1978: 87; Abbott & Dance, 1982: 189,

row 1, right fig. (4); Sander & Lalli, 1982: 313, 316, fig. 2; Snyder, 1984: 28, 30; Habe & Okutani, 1985: 193, row 1, right fig. (4); Sunderland & Sunderland, 1995: 18, 2 figs.; Goto & Poppe, 1996: 388; Hadorn, 1996: 18, 23, 24, fig. 1; Hadorn, 1997: 14; Hadorn & Rogers, 2000: 14, 39, 52, pl. 4, figs. 40, 41; Mallard & Robin, 2005: 11, pl. 18; [*non Fusinus ceramidus* (Dall, 1889), *auctt.*, Bermuda, = *Lightbournus russjenseni* n. sp.].

Fusinus (*Barbarofusus*) *ceramidus*: Abbott, 1974: 230.

Fusinus caramidus [*sic*] "(Dall)": Santos Galindo, 1977: 188; Snyder, 2003: 61.

Fusinus ceraunicus [*sic*] "(Dall)": Santos Galindo, 1977: 188; Snyder, 2003: 64.

Fusinus ceramidas [*sic*]: Okutani, 1983: 24.

Types examined: Lectotype, 46.2 mm, with operculum, Blake stn 290, Barbados, 13°11'54"N, 59°38'45"W, depth 134 m, USNM 87069; 2 paralectotypes, 18.7 & 11.3 mm, Blake stn 273, Barbados, 13°03'05"N, 59°36'18"W, 188 m, USNM 87068.

Other material examined: 5 sh, 39.0, 31.2, 30.0, 30.0 & 24.3 mm, in front of Bellair Research Institute, St. James coast, Barbados, depth 220 m, ANSP 416323; 6 sh, 51.0, 36.1, 31.3, 26.3, 19.4 & 19.2 mm, in front of Bellair Research Institute, St. James coast, Barbados, ANSP 416324; 4 sh, 43.7, 40.1, 39.7 & 35.3 mm, off west coast of Barbados, depth 165 m, dredged, ANSP 416371; 2 sh, 36.4 & 14.5 mm, west coast of Barbados, depth 90 m, WGL; 1 sh, 17.6 mm, west of Barbados, depth 166 m, WGL; 1 sh, 31.1 mm, off Barbados, depth 202 m, dredged, WGL.

Type locality: Barbados, 13°11'54"N, 59°38'45"W, depth 134 m.

Description: Shell broadly fusiform, color pale orange-pink to white, length to 51.0 mm, with about 9–10 whorls. Protoconch of about 2 whorls, tip incurved and flat, sides convex but not expanding, first 1–3/4 whorls smooth, glassy, final 1/4 whorl with 2–4 axial riblets, junction with teleoconch distinct. Teleoconch with as many as 8 rounded, subtabulate, rapidly expanding whorls ornamented with axial ribs, spiral cords, and subsutural lamellae. Suture well defined by convexity of surrounding whorls, undulating slightly in accord with adjacent axial ribs and intercostal areas, bordered anteriorly by prominent, densely imbricated axial lamellae beginning on about third teleoconch whorl and continuing to anterior end of body whorl. Axial ribs prominent, broad, extending from suture to suture on first 2–3 whorls, beginning anterior to subsutural lamellae on subsequent whorls; usually 6 ribs on all whorls, less commonly 7 or 8 on penultimate and body whorls of some shells. Spiral cords generally low, broadest atop axial ribs, narrowest near centers of

intercostal areas; first three whorls with 2–3 primary cords crossing axial ribs and 3–4 fine threads between cords; primary cords increasing by intercalation to 5 by about whorl 6, third cord strongest, creating shoulder angle on that and subsequent whorls, posterior-most cord weaker than others; about 6 primary cords on penultimate whorl, secondary threads by now weakened and barely perceptible; body whorl subquadrate, defined by shapes of large axial ribs, ribs not continuing onto siphonal process; about 9–11 spiral cords on body whorl, some considerably stronger than others.

Aperture ovate to subquadrate, constricted at posterior sinus and at junction with siphonal canal. Parietal wall thin, smooth, concave, with 1–4 weak, oblique folds near anterior end of columella and rather weak node at edge of posterior sinus, folds and nodes sometimes absent on immature shells. Outer lip thin, broadly arcuate, slightly crenulated by termini of spiral cords, internal wall with about 12–16 lirae, those toward posterior side generally smooth and entire, those toward anterior side often periodically constricted or interrupted as dashes and dots; smooth area separating tips of lirae from edge of outer lip. Anterior end of aperture constricted by anteriormost columellar plica and prominent node on inside of outer labral wall in mature shells.

Siphonal canal of mature shells moderately long, slightly curved and canted to left in apertural view, smooth within; parietal margin distinct, slightly raised, forming narrow pseudoumbilicus near tip; 12–14 thin, oblique spiral cords crossed by numerous fine axial growth increments continuing from base of body whorl to tip.

Operculum of lectotype ovo-elongate, subreniform, dimensions 10.6 × 5.5 mm, corneous, brown, with terminal nucleus; outer surface covered with densely packed microscopic growth lines; inner surface smooth, with large, ovate muscle scar surrounded by thick callus, about 6 distinct concentric growth increments evenly spaced across surface.

Radula: see Figure 3, after Bullock (1968: 107, pl. 8, fig. 7).

Distribution: Western Atlantic Ocean; southern Caribbean Sea at Barbados, Colombia, Panamá, and Nicaragua; depth range 73–220 m.

Remarks: Shells of *Lamellilaturus ceramidus* are readily separable from all other western Atlantic Peristerniinae by the combination of characters stated in the generic diagnosis. However, *L. ceramidus* shells show an interesting resemblance to several species of *Fusolatirus* from the Indo-west Pacific, especially *F. elsiae* (Kilburn, 1975) of southeastern Africa. Subsutural lamellae on shells of *L. ceramidus* are much more prominent than those on shells of *F. elsiae*, and the radula of *F. elsiae* (see Snyder and Bouchet, 2006:2, fig. 1-L) is

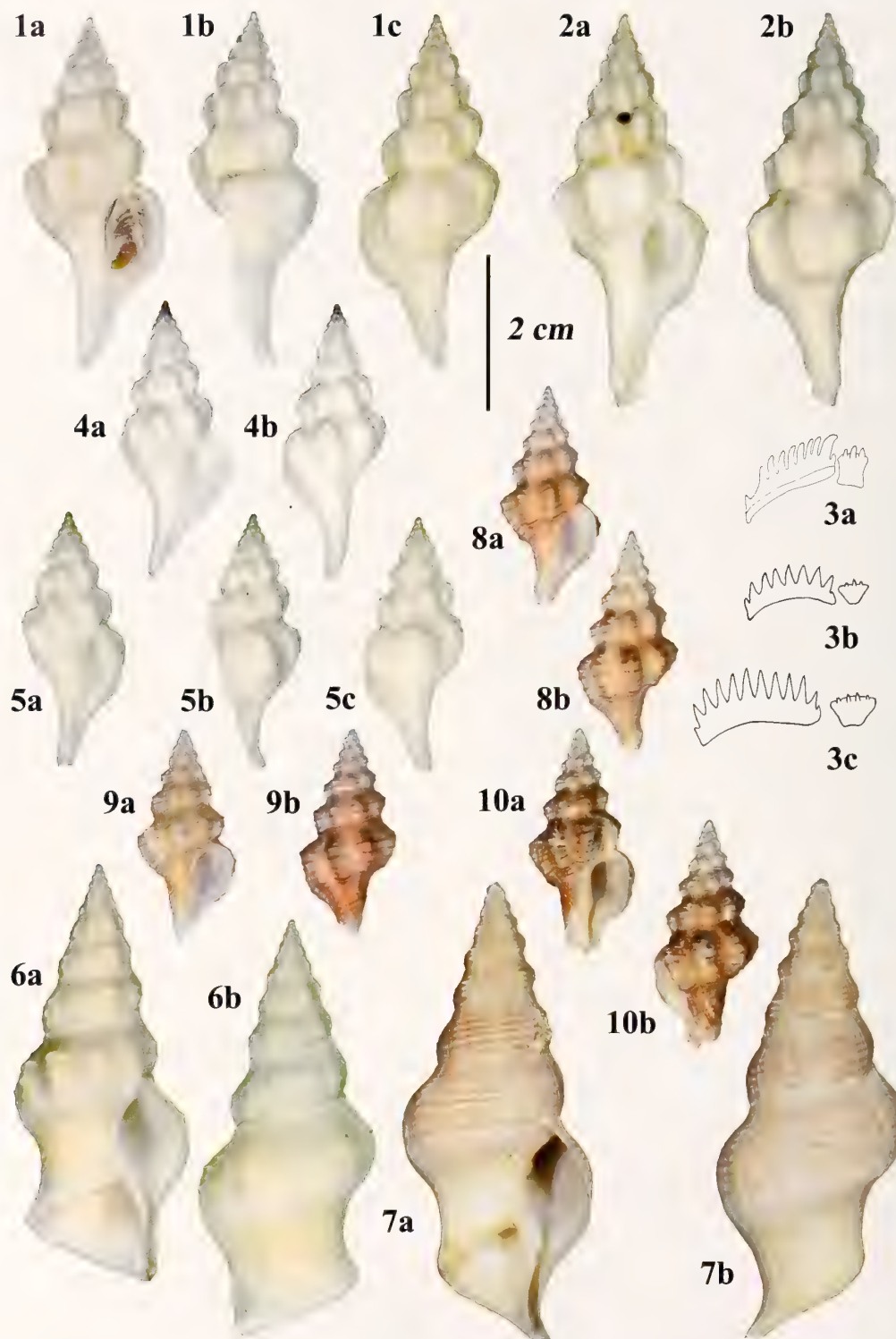


Figure 1. *Lamellilaturus ceramidus* (Dall, 1889a), lectotype, 46.2 mm, Barbados, 13°11' 54" N, 59°38'45" W, depth 134 m, USNM 87069.

Figure 2. *Lamellilaturus ceramidus* (Dall, 1889a), 51.0 mm, in front of Bellair Research Institute, St. James coast, Barbados, depth 220 m, ANSP 416323.

Figure 3a. *Lamellilaturus ceramidus* (Dall, 1889a), radula (after Bullock, 1968:pl. 8 fig. 7).

Figure 3b,c. *Fusinus colus* (Linnaeus, 1758), radula (after Barnard, 1959:fig. 19j); (b) is from an immature specimen and (c) is from a mature specimen.

decidedly *Peristernia*-like, whereas the radula of *L. ceramidus* (Figure 3) is not.

The illustration of a specimen (USNM 87069) as the holotype of *Fusinus ceramidus* (Dall, 1889a) by Abbott and Dance (1982; 1986) constituted a valid designation of lectotype according to International Code of Zoological Nomenclature Article 74b then in effect (ICZN, 1985), so a similar but later designation by Hadorn and Rogers (2000) was redundant. Dall (1890) chose this same shell to illustrate the species, and Bullock (1968) figured it as the holotype. We did not examine the two paralectotypes (MCZ 7240) that were examined by Hadorn and Rogers (2000), but we did examine the 7.2-mm syntype (MCZ 7239) that those authors identified as a probable juvenile of an unidentified *Fusinus* species. We concur that the shell is not conspecific with *Fusus ceramidus*, but we are not confident that it can be assigned to *Fusinus* or even to Fasciariidae.

Most valid records of *Lamellilaturus ceramidus* have involved the population at Barbados, but Hadorn and Rogers (2000) also reported three specimens trawled off Panamá, Nicaragua, and the Colombian Basin; photographs of the latter two specimens provided to us by Hadorn confirm their identities as *L. ceramidus*.

Records of this species at Bermuda (Snyder, 1984, 2003; Hadorn and Rogers, 2000; Mallard and Robin, 2005) are incorrect and involve one or two species that we describe as new below.

Lightbournus gen. nov.

Type species: *Lightbournus russjenseni*, sp. nov., Recent, Bermuda, designated herein.

Diagnosis: Peristerniine gastropods with small fusiform shells (lengths to 35.7 mm) and smooth, paucispiral protoconchs; whorls sculpted with broad, strong axial ribs and less prominent spiral cords; sutures distinct, not bordered by spiral threads or axial lamellae; aperture ovate, constricted anteriorly and posteriorly; parietal shield of mature shells with distinct posterior node, columella with several low but distinct, oblique folds near anterior end; inside of outer lip with well-developed lirae that are paired and entire in posterior

half of aperture, unpaired and somewhat interrupted in anterior half; siphonal canal slender, moderately extended, canted to left in apertural view; operculum and radula unknown.

Etymology: The genus name is masculine and honors J. R. H. "Jack" Lightbourn of Hamilton, Bermuda, whose ardent pursuit of Bermuda mollusks is commemorated by this and several other taxa.

Remarks: *Lightbournus*, known only by its type species, is readily distinguished from *Lamellilaturus*, with which it has been confused, by its lack of subsutural lamellae; although species of both genera have oblique columellar plicae, those of *Lamellilaturus* are broader, lower, and much less distinctly defined than those of *Lightbournus*. The anterior location and low, oblique shape of the columellar plicae distinguish species of *Lightbournus* from species of *Hemipolygona*, *Polygona*, and *Pustulaturus*, other western Atlantic *Laturus*-like genera whose columellar plicae are generally stronger, aligned more nearly perpendicular, and situated higher on the columella (see Figure 19).

Lightbournus russjenseni sp. nov.

Figures 4–5

Fusinus ceramidus: Snyder, 1984: 28, 30; Hadorn & Rogers, 2000: 14 (in part); Mallard & Robin, 2005: pl. 18, fig.; [non *Lamellilaturus ceramidus* (Dall, 1889a)].

Fusus ceramidus: Snyder, 2003: 64 (in part); [non *Lamellilaturus ceramidus* (Dall, 1889a)].

Type material: Holotype, 35.7 mm, south shore of Bermuda, depth 200–240 m, traps, ANSP 416321. Paratypes: 5 sh, 33.2, 30.2, 29.9, 27.8 & 25.0 mm, 0.8 km southeast of St. Davids, south shore of Bermuda, depth 293–366 m, USNM 819198; 1 sh, 28.2 mm, 2.4 km south of Gurnet Rock, south shore of Bermuda, depth 200–240 m, traps, ANSP 416375; 2 sh, 30.3 & 26.2 mm, same locality and depth, ANSP 416374; 1 sh, 26.9 mm, same data, KLS; 1 sh, 20.7 mm, south shore of Bermuda, depth 180–240 m, traps, ANSP 416376; 3 sh, 30.3, 26.4 & 25.7 mm, 4.0 km off

Figure 4. *Lightbournus russjenseni* sp. nov., holotype, 35.7 mm, in traps off south shore of Bermuda, depth 220–240 m, ANSP 416321.

Figure 5. *Lightbournus russjenseni* sp. nov., paratype, 33.1 mm, in traps, Bermuda, depth 220 m, BMSM 15070.

Figure 6. *Bullockus mcmurraii* (Clench & Aguayo, 1941), 42.9 mm, off West End, Grand Bahama, depth 214 m, WGL.

Figure 7. *Bullockus mcmurraii* (Clench & Aguayo, 1941), 60.0 mm, off West End, Grand Bahama, depth 402–420 m, BMSM 26305.

Figure 8. *Bullockus guesti*, sp. nov., holotype, 28.6 mm, trapped with hermit crab off south shore of Bermuda, depth 220 m, FLMNH 41161.

Figure 9. *Bullockus guesti*, sp. nov., paratype, 27.2 mm, in traps 2.4 km south of Gurnet Rock, south shore of Bermuda, depth 200–250 m, ANSP 416322.

Figure 10. *Bullockus guesti*, sp. nov., 29.7 mm, dived south of Tucker's Town, Bermuda, depth 51 m, USNM 1100736.

south shore of Bermuda, depth 220 m, DMNH 096984; 2 sh, 28.8 & 25.7 mm, same data, DMNH 187105; 1 sh, 29.0 mm, same data, DMNH 096993; 2 sh, 28.6 & 26.1 mm, same data, DMNH 202581; 1 sh, 26.5 mm, offshore of Bermuda, traps, DMNH 212752; 1 sh, 34.4 mm, Bermuda, depth 220 m, traps, HGL; 1 sh, 33.1 mm, same data, BMSM 15070; 1 sh, 32.0 mm, same data, FLMNH 41160; 2 sh, 33.0 & 29.4 mm, Bermuda, depth 220 m, traps, WGL.

Type locality: Off south shore of Bermuda, depth 200–240 m.

Description: Adult shell of moderate size, length to 35.7 mm, uniformly white, with nearly ten rapidly expanding, well-separated convex whorls. Protoconch relatively slender, of about 2-1/4 to 2-1/2 elevated whorls, first two whorls glassy, smooth, final 1/4 to 1/2 whorl with 3 or 4 rather broad axial riblets, junction with teleoconch abrupt. Nearly 8 teleoconch whorls each bearing 7, occasionally 8, broad, well-developed axial ribs crossed by less conspicuous spiral cords. Axial ribs extending from anterior suture nearly to posterior suture, slightly shouldered posteriorly, more strongly developed toward anterior suture, increasing in size anteriorly, continuing undiminished over body whorl. Suture well-defined, undulating slightly in accord with adjacent ribs and intercostal areas, rarely with faint crenulations caused by growth increments on posterior edge of adjacent anterior whorl. Spiral cords smooth, beginning at junction with protoconch; first teleoconch whorl with 4 cords, weaker 2 on posterior slope, stronger 2 crossing axial ribs, more swollen on ribs than in intercostal areas; number of cords increasing by intercalation anteriorly, about 3–4 weak ones on slope and 6 stronger ones on ribs of penultimate whorl; about 12–14 cords of more or less even strength on body whorl, continuing anteriorly onto siphonal process.

Aperture ovate-elongate, constricted near posterior sinus and at intersection with siphonal canal. Parietal wall concave, smooth, with 1–3 low, oblique folds (plicae) near anterior end of columella and single prominent node at posterior sinus. Outer lip arcuate, finely crenulate in accord with termini of spiral cords, internal wall with 10–12 prominent to weak lirae, those toward posterior half of aperture often paired, entire, those toward anterior side on mature shells often interrupted into dashes or raised dots; lirae terminating in swollen tips before reaching edge of outer lip of mature shells, interval between tips and edge smooth. Constriction at anterior end of aperture formed by anteriormost columellar fold and prominent node on labral wall of larger shells.

Siphonal canal well developed, moderately long, canted to left in apertural perspective, smooth within, with distinct parietal margin and 10–12 thin, oblique

spiral cords on outer surface, cords diminishing in strength toward tip.

Operculum and radula unknown.

Etymology: The species name honors the late Russell H. “Russ” Jensen (1918–2001), former Emeritus Head of the Mollusk Department of the Delaware Museum of Natural History and a specialist on the Mollusca of Bermuda.

Distribution: Western Atlantic Ocean; known only at Bermuda, depth range 180–366 m.

Remarks: We did not ascertain how the USNM paratypes of *Lightbournus russjenseni* were collected, but all other specimens we examined were shells brought by hermit crabs into traps set in deep water as described by Lightbourn (1991). Snyder’s (1984) report of *Fusinus ceramidus* in depths of 183–366 m was based on shells of *L. russjenseni*, including some listed among our material examined and was the basis for Snyder’s (2003) inclusion of Bermuda in the range of *Fusinus ceramidus*. More recently, Mallard and Robin (2005) published two color photographs of a Bermudan shell of *L. russjenseni* that they identified as *Fusinus ceramidus*. Hadorn and Rogers (2000) also included Bermuda within the range of *F. ceramidus*, but without indicating the source of their information; their record was probably of *L. russjenseni*. *Lightbournus russjenseni* may also have been represented among shells that Lightbourn (1991) listed as *Latirus brevicaudatus*; we examined a few *L. russjenseni* among shells received (by MAS) from Lightbourn as *L. brevicaudatus*, but most of those shells represent another new species described later in this paper.

***Bullockus* gen. nov.**

Type species: *Bullockus guesti* sp. nov., Recent, Bermuda, designated herein.

Diagnosis: Peristerniine gastropods with broadly fusiform shells of small to large size for subfamily (lengths 30–82 mm); whorls sculpted with moderate to strong axial ribs and less prominent spiral cords; sutures incised, lacking adjacent cords or lamellae; siphonal canals relatively short, slender, canted to left, with shallow pseudoumbilicus near tip; apertures ovate, constricted anteriorly and posteriorly, with parietal shields with columellar plicae absent, rudimentary, or developed only on largest mature shells; and outer lips of mature shells bearing internal lirae interrupted as dashes or dots.

Etymology: The genus name is masculine and honors Dr. Robert C. Bullock, University of Rhode Island, Kingston, RI, whose earlier studies of western Atlantic *Latirus*-like taxa paved the way for our study.

Remarks: Species of *Bullockus* differ from other *Latirus*-group species by the combination of characters defined in the diagnosis. Species other than the type species that we classify in *Bullockus* include *Latirus* (*Hemipolygona*) *mcmurraiyi* Clench and Aguayo, 1941, from northern Cuba and the northwestern Bahama Islands, depths 214–420 m (Clench and Aguayo, 1941; Lan, 1993; Sunderland and Sunderland, 1996; Petuch, 2002; Snyder, 2006; this report); *Hemipolygona honkeri* Snyder, 2006, from the southwestern Caribbean Sea and the eastern Bahamas, depths 245–550 m (Snyder, 2006); *Latirus* (*Latirus*) *varai* Bullock, 1970, from northeastern Cuba, depth 183 m (Bullock, 1974); and *Bullockus pseudovarai* sp. nov., from the eastern Bahama Islands, depths 245–550 m. All of these species share features of the columella and suture that characterize *Bullockus*.

The type species previously was mistaken for a species of *Polygona* Schumacher, 1817, but shells of that genus have prominent, near-perpendicular columellar plicae and sutures bordered with spiral cords, wrinkles, axial lamellae, or often all three. The other included species previously were classified with *Latirus* Montfort, 1810, and *Hemipolygona* Rovereto, 1899, but are distinguished from *Latirus* by having shells with angulate whorls bearing distinct spiral cords and subovate apertures and from *Hemipolygona* by lacking distinct columellar plicae and by having sutures that are finely incised between the smooth surfaces of adjacent whorls, without adjacent cords, wrinkles or lamellae.

Latirus mcmurraiyi differs from other species of *Bullockus* by having a shell with an often remarkably expanded umbilicus. This is a variable feature in several *latirid* genera. Similar aberrations are found in some specimens of *Hemipolygona recurvirostris* (Schubert & Wagner, 1829). Some shells of *L. mcmurraiyi* have a few weak, oblique folds or even small, tooth-like plicae near the anterior end of the columella, but on most shells the columella is as featureless as that of the type species of *Bullockus*; that feature and the complete lack of ornamentation around the suture prompt us to place the species in *Bullockus*. Vermeij and Snyder (2006: 417) had tentatively placed this species in *Hemipolygona*.

We observed several kinds of variation among eleven specimens of *B. mcmurraiyi* that we examined: holotype, 52.2 mm, off Matanzas, Cuba, 348 m, MCZ 135285; 1 sh, 73.5 mm, off Matanzas, Cuba, 400–420 m, KLS; 1 sh, 55.7 mm, off Tamarind, Grand Bahama Island, ANSP 368995; 2 sh, 52.3 & 39.7 mm, off Tamarind, Grand Bahama, 214 m, KLS; 1 sh, 42.9 mm, off West End, Grand Bahama, 214 m, WGL; 1 sh, 54.5 mm, off West End, 408–421 m, WGL (Figure 6); 1 sh, 41.5 mm, off West End, 26°38'N, 78°59'W, 420 m, ANSP 416377; and 3 sh, 48.6 mm (BMSM 26298),

39.0 mm (BMSM 26299) & 60.0 mm (BMSM 26305; Figure 7), all off West End, Grand Bahama, 402–420 m. The holotype and KLS shells from off Matanzas, Cuba, have weak spiral cords, causing them to appear smoother than most Bahamian shells, but cords on the WGL and two of the three BMSM shells from off West End are nearly as weak as the Cuban specimens. The columella of the holotype lacks any indication of plicae, but the other shell from off Matanzas, by far the largest specimen examined at 73.5 mm, has three low, tooth-like plicae at the anterior end of the columella; one to three rather vague columellar folds are present on the nine shells from Grand Bahama. Finally, the holotype is darkly stained (by mud?) and the large KLS shell from off Matanzas is grayish-white, but most shells from Grand Bahama are uniformly light yellow; the exceptions, two shells from off West End (BMSM 26299 & 26305; Figure 7) are covered with horizontal brown bands caused by the presence of that color over all areas not occupied by white spiral cords.

Features of *Hemipolygona honkeri* that prompt us to reclassify the species in *Bullockus* are discussed in remarks for *B. guesti*. Similarly, features of *Latirus varai* that place it in *Bullockus* are discussed with the account for *B. pseudovarai*.

***Bullockus guesti* sp. nov.**

Figures 8–10

[?] *Latirus* sp. near *sanguifluus* “Rve.” Peile, 1926: 82; Bullock, 1974: 76; [non *Latirus sanguifluus* (Reeve, 1847), Recent, Polynesia, = *Turritatirus sanguifluus*, fide Vermeij & Snyder, (2006: 419)].

Latirus brevicaudatus (Reeve, 1847). Waller, 1973: 43; Lightbourn, 1991: 5; [non *Latirus brevicaudatus* (Reeve, 1847), = *Polygona brevicaudata* (Reeve, 1847), fide Vermeij and Snyder (2006: 420)].

Type material: Holotype 28.6 × 12.8 mm, off south shore of Bermuda, depth 220 m, trapped with hermit crab, FLMNH 41161. Paratypes: 29.7 × 13 mm, south of Tucker’s Town, Bermuda, depth 51 m, dived by T. Waller, USNM 1100736; 1 sh, 27.2 mm, 2.4 km south of Gurnet Rock, south shore of Bermuda, depth 200–250 m, traps, ANSP 416322; 4 sh, 25.1, 23.1, 18.7 & 16.2 mm, south shore of Bermuda, depth 180–240 m, traps, ANSP 416373; 1 sh, 20.3 mm, same data, BMSM 15071; 1 sh, 19.3 mm, same data, KLS; 1 sh, 22.0 mm, same locality, 200–240 m, traps, ANSP 416372; 1 sh, 19.4 mm, 4.0 km off south shore of Bermuda, depth 220 m, traps, DMNH 234001; 2 sh, 20.3 & 18.5 mm, south of Gurnet Rock, Bermuda, depth 220 m, DMNH 187106; 1 sh, 21.2 mm, Bermuda, depth 220 m, traps, WGL.

Description: Shell solid, broadly fusiform, to 29.7 mm long, 13.0 mm wide, with about 10 whorls. Protoconch smooth, glassy, of about 2 whorls, with rounded tip and convex sides; final 1/2 whorl with 3–5 axial riblets of increasing strength; junction with teleoconch abrupt. Teleoconch pale orange, sometimes faded nearly white, of about 8 rapidly expanding, sharply angled whorls, with prominent axial ribs, less prominent orange-brown spiral cords, and a well-marked suture. Axial ribs about 8 per whorl, broad, abutting anterior suture and extending to, but not over, posterior sutural ramp. First teleoconch whorl with about 3 spiral cords of equal size; cords increasing by intercalation to 6 or more on second and later whorls, including about 4 smaller cords on sutural ramp and posterior halves of ribs and 2 larger cords on anterior halves of ribs, sometimes with another cord adjacent to anterior suture; 3–4 largest cords on each whorl colored dark orange-brown, contrasting with lighter background color of teleoconch; body whorl with as many as 12 dark cords, 2 cords at periphery strongest. Suture well-marked, undulating in accord with ribs and intercostal areas, without subsutural lamellae.

Aperture ovate to subquadrate; parietal wall smooth, concave, distinctly demarked on mature shells, with node-like callus at posterior sinus; columella without plicae but terminating in (usually) sharp angle at junction with siphonal canal. Outer lip arcuate, finely crenulate in accord with termini of spiral cords, internal wall with 8–10 well-developed lirae, posterior lirae entire, anterior ones interrupted as dashes or dots on mature shells, lirae not extending to lip edge; node at anterior end usually prominent, uncommonly reduced, together with columellar terminal angle forming constriction between aperture and siphonal canal.

Siphonal canal rather short, slender, canted to left in apertural view, smooth within; edge of parietal callus distinct, raised on larger shells, forming shallow, chink-like pseudoumbilicus near anterior tip; about 7 dark or lighter smooth oblique cords continuing from base of body whorl to tip.

Operculum (of paratype USNM 11000736) ovate, brown, corneous, dimensions 5.4×3.6 mm, nucleus terminal, with concentric growth increments on upper surface and muscle scar bordered by conspicuous callus beneath, callus wider and thicker near nucleus. Radula unknown.

Distribution: Western Atlantic Ocean; known only at Bermuda, depth range 51–250 m.

Etymology: The species name honors the late Arthur Tucker Guest, O. B. E. (1907–1993), retired customs officer and student extraordinaire of the shells of Bermuda, who was instrumental in collecting and distributing most shells that we examined.

Remarks: Except for the USNM paratype collected at a depth of 51 m using scuba (Waller, 1973:fig. 11), all specimens we examined of *Bullockus guesti* were occupied by hermit crabs taken in traps set in deeper water as described by Lightbourn (1991). The depth of collection of Waller's specimen is much shallower than any other recorded for the species and is the only depth where a living specimen has been collected.

Shells of *B. guesti* have been confused with *Polygona brevicaudata* (Reeve, 1847). Although their shells are similar in general profile, in sculpture of the axial ribs, and particularly in having orange-brown spiral cords, *P. brevicaudata* can be distinguished by having distinct, well-developed, near-perpendicular plicae on its columella and rugose wrinkles, often overlain by fine axial lamellae, just anterior to its suture.

The only reports of *Latirus* living at Bermuda involve Peile's (1926) uncertain listing of "*Latirus* sp. near *sanguifluus* (Rve.)," Waller's (1973) listing of *Latirus brevicaudatus* from a depth of 51 m off the southern coast, and Lightbourn's (1991) mention of crabbed shells of *L. brevicaudatus* among specimens trapped in deep waters off the southern coast. Bullock (1974) proposed that Peile's record may have been based on *Latirus angulatus* (Röding, 1798), in which he included *L. brevicaudatus* as a junior synonym. "*Latirus*" *sanguifluus* (Reeve, 1847), reclassified as *Turritulus sanguifluus* by Vermeij and Snyder (2006), is a Polynesian species endemic to the Tuamotu and Marquesas Archipelagos (Salvat and Rives, 1975) and is unlikely to occur at Bermuda. Bullock (1974) also proposed that Waller's record of *L. brevicaudatus* represented *L. angulatus*, but we re-examined that specimen (USNM 1100736), which is *B. guesti*.

The "*L. brevicaudatus*" of Lightbourn is also *B. guesti*, as evidenced by shells received from Lightbourn and Guest, and all specimens except Waller's that we examined originated from that source. Thus, it seems likely that all reports of Recent *P. brevicaudata* at Bermuda were actually of *B. guesti*. Reports of *L. brevicaudatus* in Bermuda Pleistocene deposits are errors for a species of *Leucozonia* (see discussion).

Shells of *Bullockus guesti* most resemble those of *B. honkeri*, (Figure 14), but shells of the latter species are uniformly yellow and larger (to 55.5 mm, versus 29.7 mm for *B. guesti*), with larger protoconchs, whorls with more prominent spiral cords, colored the same as other exterior surfaces, that protrude and create the appearance of points where they cross axial ribs, and several inconspicuous folds on the columella.

Bullockus pseudovarai sp. nov.

Figures 11,13

Latirus varai: Snyder, 2006: 41; [non *Latirus* (*Latirus*) *varai* Bullock, 1970, Recent, northeastern Cuba].



Figure 11. *Bullockus pseudovarai*, sp. nov., holotype, 82.3 mm, off San Salvador, Bahama Islands, depth 488 m, ANSP 416379.
Figure 12. *Bullockus varai* (Bullock, 1970), possible paratype, 57.2 mm, off Gibara, Oriente Province, Cuba, depth 183 m, KLS.
Figure 13. *Bullockus pseudovarai*, sp. nov., paratype, 64.7 mm, off San Salvador, Bahama Islands, depth 220–550 m, ANSP 416378.
Figure 14. *Bullockus honkeri* (Snyder, 2006), holotype, 39.6 mm, off San Salvador, Bahama Islands, depth 245–550 m, ANSP 413204.

Hemipolygona varai: Snyder, 2006: 44, pl. 1, figs. 1a–d, 2a–d; [*non Latirus (Latirus) varai* Bullock, 1970].

Type material: Holotype 82.3 × 27.7 mm, from off San Salvador, Bahama Islands, depth 488 m, ANSP 416379; paratype 64.7 mm, off San Salvador, Bahamas, depth 220–550 m, ANSP 416378.

Type locality: Off San Salvador, eastern Bahama Islands, 488 m.

Description: Shell solid, relatively large (to 82.3 × 27.7 mm) fusiform, with about 11 whorls. Protoconch of about 2 smooth, glassy whorls, with rounded tip and convex sides, about 4 axial riblets on final 1/2 whorl; junction with teleoconch abrupt. Teleoconch white with prominent orange-brown axial ribs and other patches of similar color scattered on body whorl; about 9 postnuclear whorls increasing in size anteriorly; axial ribs well developed, 7 ribs on early whorls, increasing to 8 by about whorl 5; ribs aligned in transverse rows between whorls beginning at about whorl 5. Spiral cords 3 on first whorl, of about equal size, anterior-most 2 cords stronger than others thereafter, creating “squared” effect where they cross ribs and conferring tabulate appearance to spire; number of cords increasing to 4 on about whorl 5, with some barely perceptible secondary threads between, middle 2 cords strongest, resembling points where they cross ribs; about 11 cords of varying strength on body whorl, 2 cords at shoulder much stronger than others. Suture incised, distinct, undulating slightly in accord with adjacent ribs and interspaces, bordered above and below by essentially smooth shell surfaces interrupted only by very fine, irregularly spaced axial growth increments.

Aperture ovate, white, with slight anterior and posterior constrictions; parietal wall essentially smooth, concave, slightly thicker at posterior sinus; columella bearing single, inconspicuous, oblique fold, arching anteriorly in gradual transition to siphonal process. Outer lip arcuate, marked with 2 points near shoulder and lesser crenulations elsewhere in accord with termini of spiral cords of body whorl; internal wall with as many as 20 lirae of unequal size, some terminating before others, none extending to edge of lip, termini of farthest extending lirae punctuated with extra dots at end; prominent node at anterior edge of liral array, forming constriction at entrance to siphonal process.

Siphonal canal rather short, slender, canted to left in apertural view, smooth within; inner edge (continuation of parietal wall) distinct, raised, forming shallow, slender pseudoumbilicus near anterior tip; about 8 white, oblique cords continuing from base of body whorl to tip, diminishing in strength anteriorly.

Operculum brown, corneous, fairly slender, curved and tapering anteriorly to terminal nucleus; outer

surface marked with numerous closely packed, arc-like concentric growth increments; inner surface with muscle scar bearing concentric elliptical rings of growth, surrounded by thick ring of callus.

Radula unknown.

Etymology: The name *pseudovarai* is formed of the Greek prefix *pseudes*, meaning false, and *varai*, the name of a similar species; literally, the false *varai*, referring to a report by Snyder (2006) in which the new species was mistakenly figured and discussed as *Hemipolygona varai*.

Distribution: Western Atlantic Ocean; known only from near San Salvador, Bahama Islands, depths 220–550 m.

Remarks: Snyder (2006: 44, pl. 1, figs. 1, 2) figured two specimens of *Bullockus pseudovarai* as *Hemipolygona varai*, a closely related species from northeastern Cuba. The smaller of the specimens (64.7 mm) that Snyder figured is the paratype of the new species; the larger of the shells (75.2 mm) is in the collection of Tom Honker of Delray Beach, Florida. The only variations noted among those two shells and the holotype is that the anterior-most of the two shoulder cords on the 75.2-mm shell is somewhat weaker than the posterior cord, conferring to the whorl a less “squared” profile; the axial ribs are less aligned with each other on consecutive whorls of the 75.2-mm shell than on the other two.

Snyder (2007) shows that the name *Latirus varai* was incorrectly applied by Pointier & Lamy (1998: 131) and Mallard & Robin (2005: pl. 51) to shells from the Lesser Antilles, and Snyder has reclassified that species in the genus *Hemipolygona*. A shell from Venezuela that Mallard & Robin (2005: pl. 51) also figured as *Latirus varai* appears to be undescribed.

We believe that the only valid reports of *Latirus varai* involve the 70 mm holotype and a paratype from off Gibara, Oriente Province, Cuba, in 183 m. The holotype, MCZ 262589, has been illustrated by Bullock (1970: text-fig. 1), Abbott (1974: text-fig. 2493a), Kaicher (1978: card 1838), Abbott & Dance (1982, 1986: 186, row 1, right fig.), Petuch (1987: pl. 8, fig. 13), Snyder (2000: fig. 3), and Vermeij & Snyder (2006: 418, fig. 3A). The paratype, which remained in the collection of John Finlay of Wilmington, Delaware, has not been figured. A specimen of *Latirus varai* from off Gibara in 183 m that was acquired from Finlay by the Sunderlands was illustrated by Sunderland & Sunderland (1996: 17). We expected that shell to be the sole paratype, but its size is 57.2 mm, not 52.4 mm as reported for the paratype by Bullock. Whatever its status may be, the Sunderland shell is clearly conspecific with the holotype and we reillustrate it here (Figure 12) for comparison with *B. pseudovarai*.

Bullockus varai can be distinguished from *B. pseudovarai* by having many more white spiral cords crossing the brown axial ribs; the Sunderland shell has 5 cords crossing ribs on teleoconch whorls 3 and 4, 7 cords on whorls 5 and 6, 9 cords on whorl 7, and 12–13 cords on the body whorl. The cords are smaller and more closely spaced than those of *B. pseudovarai* and, because of their subequal size, do not create the “squared” profile seen on *B. pseudovarai*. Instead, the ribs of *B. varai* are rather evenly convex. We concur with Bullock’s (1970) observation that the general appearance of the ribs of *B. varai* is much like that of *Latirus kandai* Kuroda, 1950 (= *Fusolatirus kandai*; Recent, Japan and Philippine Islands), but ribs of *B. pseudovarai* certainly do not resemble those of *F. kandai*.

Bullock (1970: 134) described four folds, “the upper one weaker,” on the holotype of *B. varai*, and two of those folds are evident in the original figure. However, folds of *B. varai* are weaker, more oblique, and more anteriorly situated than are the near-perpendicular folds (plicae) of *Hemipolygona* and *Polygona* species. The Sunderland shell has no folds on its columella, evidently because it is less mature. General shell shape, including those of the protoconch, the columella, the featureless shell surfaces around the sutures, and the form of the siphonal process all dictate placement of *Latirus varai* in *Bullockus*.

DISCUSSION

All of the species treated herein have been associated at some time with *Latirus* Montfort, 1810, a generic name that has served as an umbrella for a diverse array of taxa distributed throughout tropical and subtropical regions of the world. As consequences of recent revisions noted in the introduction, many and in fact most of those species are now classified elsewhere, leaving relatively few Indo-west Pacific species and no western Atlantic species in *Latirus* (see Vermeij and Snyder, 2006). New World species until recently classified in *Latirus* are now placed in *Polygona*, *Hemipolygona*, and *Pustulaturus*, genera whose shells, together with those of *Leucozonia* and *Opeatostoma* Berry, 1958, have columellas bearing three or more well-developed, near-perpendicular plicae (Figures 15–18). Prominent columellar plicae also occur on shells of all species of the Indo-west Pacific genera *Turritaturus*, *Latirolagena* Harris, 1897, and *Peristernia* Mörch, 1852, and on most species of *Latirus* as construed by Vermeij and Snyder (2006). These plicae are prominent even on shells not yet mature. Such plicae do not occur on species of the Indo-west Pacific genera *Benimakia* or *Fusolatirus*, nor do they occur on the new genera *Lamellilaturus* and *Lightbournus*. Plicae may occur, uncommonly, on some mature shells of *Bullockus varai*,

and *B. mcmurrayi*, but most shells of that species lack plicae, and no plicae have been seen on mature shells of *B. guesti*, *B. honkeri*, or *B. pseudovarai*.

The marine molluscan fauna of Bermuda clearly is derived from the Caribbean region (Jones, 1876), but its remote location and cool winter climate seem to have acted as impediments to recruitment by many species. Groups such as the Fascioliariidae, with direct development or only brief planktotrophic larval stages, have shown very limited success recruiting to Bermuda. Although many species of Fascioliariidae are known from the Caribbean Sea and Gulf of Mexico, only three (*Fusinus lightbourni* Snyder, 1984; *Lightbournus russjenseni*, sp. nov.; and *Bullockus guesti*, sp. nov.) are known to live at Bermuda today, all in fairly deep water (~50–250 m) and all evidently endemic to Bermuda. Although we have identified no close relative of *L. russjenseni*, the nearest relative of *F. lightbourni* seems to be *F. schrammi* (Crosse, 1865) from deep water in the northeastern Antilles, and *B. guesti* belongs to a group that includes several species that live in deep waters (183–550 m) of the Bahama Islands, Cuba and the southwestern Caribbean Sea (Snyder, 2006).

If there are no shallow-water fascioliariids living at Bermuda today, historical records and reports of Pleistocene fossils suggest that a few such species reached that remote island, located ~1000 km to the east of North America (Muhs *et al.*, 2002). Shallow-water Caribbean species reported from Bermuda include *Fasciolaria distans* Lamarck, 1816 (= *Fasciolaria lilium* Fischer von Waldheim, 1807), reported by Jones (1864, 1876); *Fasciolaria tulipa* (Linnaeus, 1758), reported by Moore and Moore (1946) and Richards *et al.* (1969); *Leucozonia nassa* (Gmelin, 1791) and its junior synonym *L. cingulifera* (Lamarck, 1822), reported by Heilprin (1889), Peile (1926), and Moore and Moore (1946); and *Latirus brevicaudatus* (Reeve, 1847), reported by Richards *et al.* (1969) and Waller (1973). Dall (1889b) tentatively listed Bermuda within the range of *Leucozonia ocellata* (Gmelin, 1791), but that listing has not been substantiated. There are also two unfortunate Bermuda listings of the Indo-west Pacific *Pleuroploca trapezium* (Linnaeus, 1758) by Santos Galindo (1977: 190, 372) but those listings are obviously spurious and may be ignored.

Fasciolaria tulipa and *Leucozonia nassa* are the two most widely ranging western Atlantic fascioliariids; *F. tulipa* occurs now from northeastern Brazil to North Carolina, and *L. nassa* ranges from Trindade Island, 1140 km off the Brazilian coast (Vermeij and Snyder, 2002) and throughout central and northern Brazil to North Carolina (Nathanson, 2006). Despite limitations imposed by their modes of reproduction and dispersal, these species have demonstrated abilities to recruit over distances that seem to constitute barriers for most other



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- Figure 15. *Pustulaturus mediamericus* (Hertlein & Strong, 1951), 78.0 mm, off Acapulco, Mexico, ANSP 416383.
 Figure 16. *Hemipolygona armata* (A. Adams, 1855), 47.7 mm, Goree Island, Dakar, Senegal, depth 15–30 m, ANSP 416384.
 Figure 17. *Polygona infundibulum* (Gmelin, 1791), 70.7 mm, Cabo de la Vela, Guajira, Columbia, depth 60 m, ANSP 416385.
 Figure 18. *Bullockus mcMurrayi* (Clench & Aguayo, 1941) 55.6 mm, Tamarind, Grand Bahama Island, depth 245 m, ANSP 368995.
 Figure 19. *Lightbournus russjenseni*, sp. nov., holotype, 35.7 mm, in traps off south shore of Bermuda, depth 200–240 m, ANSP 416321.

fascioliids, so their presence in Bermuda may seem reasonable. However, although reports indicate that both species may have arrived at Bermuda from time to time, each has encountered difficulty establishing a population there.

Fasciolaria was first reported at Bermuda by Jones (1864), who cited *F. distans* as rare based on one specimen "in a semifossil state." Jones (1876) reiterated that record and added that his marine specimens had been identified by the well known conchologist C. B. Adams, although Adams died in 1853 (Abbott, 1973), more than a decade before Jones published his first list. The Jones record was repeated by Dall (1885; 1889a, b), Heilprin (1889), and Verrill (1907). Peile (1926) also repeated the fossil record of *F. distans* and added that the species still lived at Bermuda but was rarely found; Peile's was the last report of *F. distans* at Bermuda. The next record of *Fasciolaria*, by Moore and Moore (1946), reported *F. tulipa* as occurring both fossil and living at Bermuda, although the new records were implicitly of fossil shells which had been identified by W. J. Clench. Moore and Moore noted the shells to be fairly common in subsurface calcareous sandstone cut by harbor dredging from below sea level in and around Castle Harbour, the age of the sandstone being considered "preglacial" or possibly a result of rising sea level within a glacial period. Abbott (1958) later treated the report of *F. distans* by Peile (1926), and implicitly others, as *F. tulipa* and repeated earlier comments that living specimens were rare at Bermuda. Finally, Richards *et al.* (1969) reported new records of *F. tulipa* in the Pleistocene Belmont Formation (age ~200 ka; Muhs *et al.*, 2002) of Bermuda but noted that the species is not living in Bermuda waters today, an observation reinforced by Sterrer (1998). Thus, it seems to have been decided that the original report of *F. distans* as a Bermuda fossil was an error for *F. tulipa*, that the sole evidence of living *Fasciolaria* at Bermuda was Peile's unsubstantiated note, and that no species of *Fasciolaria* now lives at Bermuda.

We have not seen any museum specimens of Recent *Fasciolaria* at Bermuda, but we did examine a voucher (ANSP 59434) from Watch Hill Park, Bermuda, that Richards *et al.* (1969) reported as a Quaternary fossil of *F. tulipa*. The specimen is an upper fragment of a spire, height 25.0 mm, with its early whorls intact. The specimen is not fascioliid but may be a fragment of a species of Cassidae, perhaps *Casmaria*. This finding refutes the only record of *Fasciolaria* at Bermuda known to be supported by physical evidence and provokes uncertainty about other Bermuda records of the genus.

Richards *et al.* (1969) also reported Bermuda Pleistocene records of *Latirus brevicaudatus* at Spencer's Point (Spencer's Point Formation, age $130,000 \pm 15,000$ ybp) and Grape Bay (Devonshire Formation; =

Devonshire marine member of Rocky Bay Formation, age ~125 ka; Muhs *et al.*, 2002), and they noted that a report by Moore and Moore (1946) of fossil *Leucozonia cingulifera* Lamarck in Castle Harbour dredgings may instead have been *L. brevicaudatus*. Based on the report by Richards *et al.*, Muhs *et al.* (2002: 1372) cited *Latirus brevicaudatus* as one of three extralimital southern (warm-water) gastropod species that ranged northward to Bermuda during the last interglacial period but do not live around Bermuda today.

We examined specimens representing both of the Richards *et al.* records, now catalogued as *Latirus* sp. at the Academy of Natural Sciences of Philadelphia. The voucher from Spencer's Point (ANSP 61785) is a small shell fragment consisting of most of a body whorl and including the aperture and columella. Prominent features include a few large, nodose ribs on the shoulder crossed by 2 fairly prominent spiral cords, followed anteriorly by 5–6 much lower cords and 1 markedly larger cord near the anterior edge of the whorl. There are about 7 finer spiral threads on the subsutural ramp but no indication of subsutural lamellae. The columella has 3, possibly 4 near-perpendicular plicae. The voucher from Grape Bay (ANSP 61768) is a larger (36.3×21.2 mm), nearly intact shell missing only the anterior end of the siphonal process but encased in limestone concretions over much of the outer surface and aperture. There are about 8 node-like ribs per whorl; several small, narrow cords on the subsutural ramp are overlain by microscopic growth increments, and the columella is obscured by concretion. We compared both vouchers with Recent *Leucozonia nassa* in the ANSP collection and judge them to be conspecific.

These fossils constitute the only physical evidence we have seen of the presence of *Leucozonia nassa* at Bermuda. Heilprin (1889: 168) first reported *L. nassa* (as *L. cingulifera*) at Bermuda without comment, indicating that he did not consider the occurrence noteworthy, and Peile (1926) also listed *L. cingulifera* among Bermudan mollusks collected by him and Arthur Haycock. Moore and Moore (1946) mentioned *L. cingulifera* as rare among living fauna of Bermuda and also reported shells from two "preglacial" [Pleistocene] beds there. But then Richards *et al.* (1969) suggested that Pleistocene records by Moore and Moore were actually of *L. brevicaudatus*, casting doubt on other previous records, none of which can now be substantiated. No more reports of *L. nassa* at Bermuda since those by Moore and Moore have been forthcoming, but our findings support those earlier reports and refute the Pleistocene records of *Latirus brevicaudatus*. Having also refuted one fossil record of *Fasciolaria tulipa* by Richards *et al.* and knowing of no other specimens of that species to demonstrate its Bermuda occurrence, we conclude that *L. nassa* may be the only

shallow-water Caribbean fascioliariid species to have recruited to Bermuda since before the onset of the last ice age.

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Injuries on Nautilus Jaws: Implications for the Function of Ammonite Aptychi

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Abstract. Documentation of repaired injuries and abnormalities on the jaws of modern nautilus sheds light on the ecology and behavior of these animals. It also helps elucidate the function of ammonite aptychi, which are traditionally interpreted as opercula. We examined 219 pairs of jaws belonging to *Nautilus belauensis*, *N. macromphalus*, *N. pompilius*, and *Allonautilus scrobiculatus*. Abnormalities occur in 68% of the sample and are only present on the lower jaw. The abnormalities consist of 1) repaired fractures, 2) small depressions, 3) radial grooves and ridges, and 4) flexures in the chitin. These abnormalities are either the result of injury or growth pathology. Injuries may be due to accidents during feeding (e.g., biting down on a hard crustacean carapace) or from predatory attacks. Alternatively, they may have been sustained during mating behavior or fighting between males. Most abnormalities occur on the left side of the lower jaw. This may be related to the fact that in male nautilus, the jaws are displaced to the right side of the midline, so that during mating, for example, the apex of the jaws of the male lines up with the left side of the jaws of the female. The presence of injuries and other abnormalities on the jaws of nautilus suggest that similar features on aptychi may have been produced during the normal use of the jaws, and do not necessarily imply an opercular function. Alternatively, aptychi may have served to strengthen and reinforce the lower jaw.

INTRODUCTION

Aptychi are present in many Jurassic and Cretaceous ammonites, mainly the Ammonitina and Ancyloceratina (Lehmann, 1980; Engeser and Keupp, 2002; Tanabe and Landman, 2002; Landman et al., 2006). Aptychi are pairs of calcitic plates that cover the outside surface of the outer lamella of the lower jaw (Figure 1A). Traditionally, aptychi have been interpreted as opercula (Trauth, 1927–1936; Schindewolf, 1958; Seilacher, 1993; Keupp, 2007), but the discovery of aptychi with other elements of the buccal mass demonstrated their homology with the lower jaws of present-day cephalopods (Lehmann, 1975, 1980). Nevertheless, the opercular theory has never been completely discarded, and as a compromise, Lehmann and Kulicki (1990) have suggested a double function, with aptychi serving as both jaws and opercula. According to these authors, the aptychus was capable of rotating into a nearly vertical position to act as an operculum in the event of an attack by a predator.

The main pieces of evidence for the interpretation of aptychi as opercula are (1) the close match between the size and shape of the aptychus and the aperture of the ammonite, 2) the calcitic composition and ornamentation of the aptychus, suggesting a protective function, and (3) the presence of repaired injuries on the

aptychus. Such injuries have been interpreted by Engeser and Keupp (2002) as resulting from predatory attacks. This assertion implies that injuries are only present on opercula, not jaws. The protective function of opercula in gastropods is well known (see, for example, Vermeij and Williams, 2007, and references therein).

In order to evaluate the significance of repaired injuries on aptychi, we studied the externally shelled cephalopod nautilus to determine if repaired injuries or other abnormalities are present on the jaws of these animals. The function of the jaws in nautilus is known. They serve for biting and tearing food. An opercular function is performed instead by the fleshy hood, which is composed of thick connective tissue. The presence of repaired injuries on the jaws of nautilus would imply that injuries, by themselves, are not sufficient proof of an opercular function. Such injuries could equally result from trauma to the jaws during the lifetime of the animal.

The presence of injuries on nautilus jaws also provides insights into the ecology of these reclusive organisms. Because of the deep water habitat of nautilus, direct observations of their behavior are problematic. As a result, investigators have relied on indirect evidence, including analyses of the isotopic

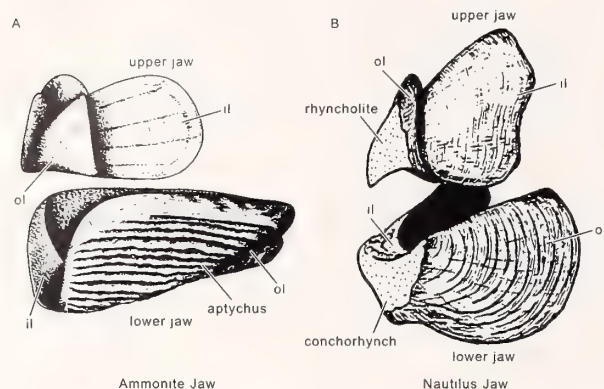


Figure 1. Comparison of the jaws of ammonites with those of modern nautilus. A. Reconstruction of the upper and lower jaws of the Early Jurassic ammonite *Hildoceras* (after Lehmann, 1975: fig. 4). Note that the lower jaw is covered with a pair of calcareous plates, known as an aptychus. il = inner lamella; ol = outer lamella. B. Upper and lower jaws of nautilus (after Tanabe and Fukada, 1999: fig. 19.3). The tips of the jaws are reinforced with calcareous deposits. il = inner lamella; ol = outer lamella.

composition of the shell (e.g., Cochran et al., 1981) and studies of repaired injuries (e.g., Arnold, 1985), for clues about their life history and habitat,

MATERIAL AND METHODS

The upper and lower jaws of nautilus are composed of chitin and each consists of inner and outer lamellae (Figure 1B). The upper jaw sits inside the lower jaw. The oral opening is surrounded by the labial margin ("lips"). The outside surfaces of the outer lamellae of the upper and lower jaws are mostly covered by a thin membrane of connective tissue and epithelium (Tanabe and Fukuda, 1999). In contrast, the inside surface of the outer lamella and the outside surface of the inner lamella of the lower and upper jaws are covered with muscles. The jaws are reinforced with calcareous deposits at the apex, known as rhyncholites and conchorhynchs (for a more complete discussion of the orientation and terminology of nautilus jaws, see Saunders et al., 1978).

We studied 219 pairs of nautilus jaws in the collections of the American Museum of Natural History (AMNH). All of the jaws are presumably from adult specimens. Part of the sample (164 specimens) consisted of the entire buccal mass preserved in alcohol. The other 55 pairs of jaws were already separated from the buccal mass and subsequently dried. In the alcohol preserved specimens, the upper jaws were still covered by tissue and were not examined for marks. However, in the dried specimens, both the upper and lower jaws were inspected. The jaws belong to four species of *Nautilus*: 141 jaws of *Nautilus macromphalus* from New Caledonia (57 males, 44 females, 40 *indet.*); 34

jaws of *Nautilus belauensis* from Palau; 42 jaws of *Nautilus pompilius* from various localities (3 from Samoa, 4 from Indonesia, 3 from Fiji, 24 from Papua New Guinea, 8 from the Philippines); and 2 jaws of *Allonautilus scrobiculatus* from Papua New Guinea.

In addition to repaired breaks, we recorded the presence of other abnormalities on the jaws. Specimens were analyzed under the stereomicroscope (x6–x50) and six specimens were observed with SEM. Because of the loss of flexibility of the chitin after drying, some parts of the jaws were broken. These breaks were easy to recognize because of the freshness and sharpness of the fractures.

RESULTS

Description of Abnormalities

We categorized the abnormalities observed on the nautilus jaws as follows: (1) repaired fractures, (2) depressions, (3) radial grooves and ridges, and (4) flexures. A total of 149 specimens (68%) of the sample exhibit at least one of these abnormalities. Almost all of the abnormalities occur on the outer lamella of the lower jaw. No abnormalities are present on the upper jaw.

1) Repaired fractures: The most spectacular repaired fracture appears on a lower jaw of *Nautilus belauensis* (AMNH 51881). The jaw is 39 mm long and is undoubtedly from an adult specimen. The injury occurs on the left side of the outer lamella and extends from the anterior dorsal part of the wing to the posterior ventral part (Figure 2A, B). The break continues onto the inner lamella (Figure 2C). The outside of the outer lamella is fractured, with a maximum offset of 1.3 mm on each side of the break. On the inside of the outer lamella, the fracture is repaired by an elongate, cordlike thickening of chitin (Figure 2C, D). This chitinous thickening is 2.2 mm wide and 1.0 mm high and subdivides for part of its length. There are no growth lines on the thickening and the texture is reminiscent of pahoehoe lava.

2) Depressions: Small depressions are present on some of the nautilus jaws (Figure 3C–F, I, J). These features only occur on the outside of the outer lamella of the lower jaw. Several depressions may occur on the same specimen (Figure 3E, F). The depressions are less than 1 mm long and less than 0.2 mm deep. They vary in shape from triangular to quadrate to round. They are conformable with the surrounding jaw surface, but show a slightly different texture. The depressions are not expressed on the inside surface of the outer lamella. They occur in all of the nautilus species but are more common in *Nautilus pompilius* and *N. belauensis*. They preferentially occur on the left side of the outer lamella in these species.

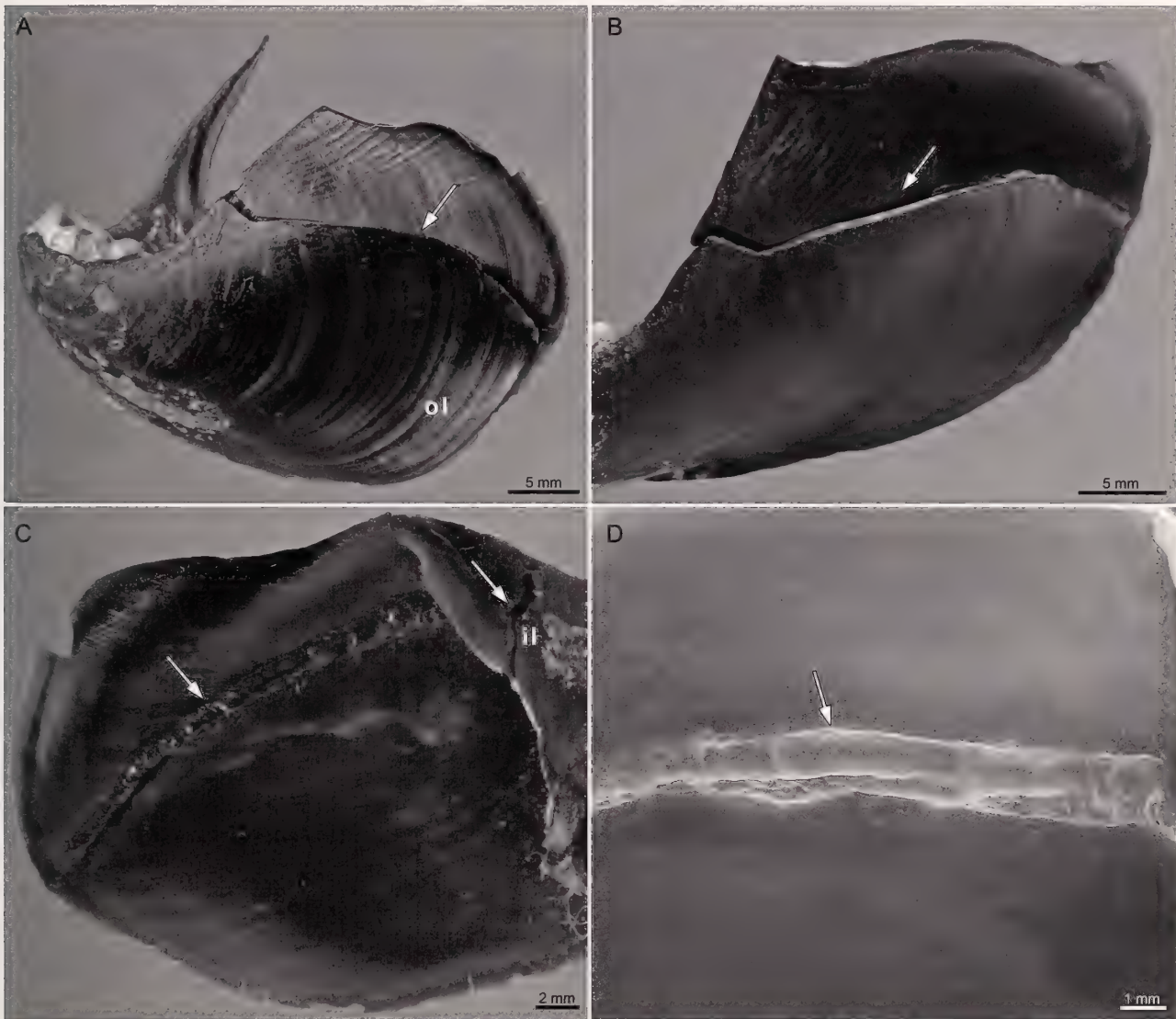


Figure 2. Lower jaw of *Nautilus belauensis* (AMNH 51881) with a large repaired injury. A. Left lateral view of the lower jaw, showing the break (arrow) on the outer lamella (ol). The break extends to the posterior end of the wing. Part of the calcareous deposit at the tip was broken away during handling. Anterior direction to the left. B. Left lateral view of the lower jaw, slightly tilted down, to expose the gap at the break (arrow). C. View of the inside surface of the outer lamella, showing the repaired portion (left arrow). Note that the break (right arrow) continues onto the inner lamella (il). Anterior direction to the right. D. Close-up of the repair (arrow) on the inside surface of the outer lamella, which consists of a thickened ridge of chitin that must have been secreted from the inside.

3) Radial grooves and ridges: As noted by Saunders et al. (1978), the outside surface of the outer lamella of the lower jaw is covered with closely spaced, comarginal lirae, which are usually interpreted as growth lines. In some specimens, however, these growth lines are transected by elongate grooves that occasionally extend to the posterior margin (Figure 3A, B). These grooves are generally superficial with a maximum depth of approximately 0.2 mm, and are usually bordered by thin ridges. Sometimes, instead of grooves, the surface is marked by thin bands, approximately 0.5 mm wide,

characterized by an irregular texture (Figure 3G, H). Radial grooves or bands occur in 54% of the specimens that show abnormalities.

4) Flexures: Flexures are minor discontinuities in the outer lamella of the lower jaw, which follow the course of the lirae (Figure 3K, L). They are sometimes expressed as overhanging fringes of chitin, indicating the previous position of the jaw margin. Flexures are very common and preferentially occur on the left side of the lower jaw (92% of the specimens with flexures).

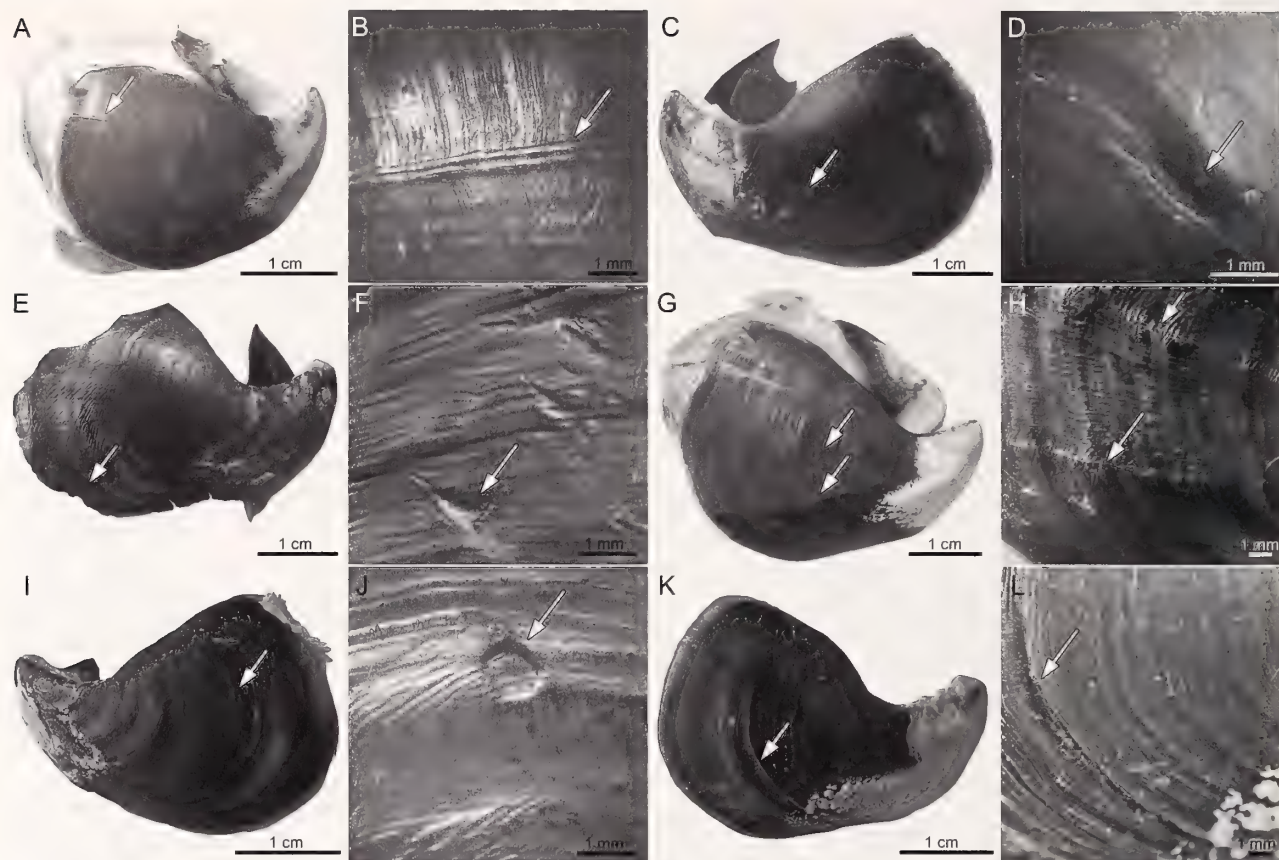


Figure 3. Abnormalities on the lower jaws of nautilus. A, B. Radial groove (arrow) on the outer lamella of the lower jaw of *Nautilus macromphalus* (AMNH 51870). The groove extends to the posterior margin of the wing, suggesting permanent damage to the jaw-secreting tissue. Anterior direction to the right. The close-up in B is rotated 180° relative to A. C, D. Elongate depression (arrow) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51868). Anterior direction to the left. E, F. Triangular depression (arrow) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51335). Anterior direction to the right. G, H. Radial bands (arrows) on the outer lamella of the lower jaw of *Nautilus belauensis* (AMNH 51883). Anterior direction to the right. I, J. Small depression (arrow) on the outer lamella of the lower jaw of *Nautilus pompilius* (AMNH 51869). Anterior direction to the left. The close-up in B is rotated 180° relative to I. K, L. Flexure in the chitin (arrow) on the outer lamella of the lower jaw of *Nautilus macromphalus* (AMNH 51884). Anterior direction to the right. The calcareous tips of the jaws are occasionally missing in these specimens due to breakage during drying or handling.

Distribution of Abnormalities

The incidence of abnormalities varies among the different species. The highest percentage of abnormalities occurs in *Nautilus belauensis*, including the specimen with the conspicuous scar. The highest percentage of grooves appears in *N. macromphalus*. The percentage of depressions is higher in *N. belauensis* and *N. pompilius* than in the other species. In *N. macromphalus*, in which the number of males and females is known, the incidence of abnormalities is higher in males than in females (70% versus 55%). The most common abnormality in both sexes is grooves. However, the incidence of grooves is higher in males than females (60% versus 36%).

Some of these differences may be related to the preservation of the jaws (alcohol versus dry). For

example, most of the flexures occur in alcohol-preserved rather than dry specimens (92% versus 8%), perhaps because flexures are less noticeable on dry specimens. In contrast, depressions are more common on dry specimens. Therefore, the kind of preservation may bias the results.

DISCUSSION

The abnormalities described on the jaws of nautilus are either the result of injuries to the jaws or growth pathologies. The repaired break in AMNH 51881 is the most obvious example of a repaired injury in which the lower jaw was broken and repaired during life by the secretion of additional chitinous material from the inside. The depressions, with a maximum depth of 0.2 mm, may also represent injuries due to impact, or

possibly damage caused by parasites. In any event, the damage was not permanent. In contrast, the radial grooves and ridges extending to the posterior margin of the jaws imply permanent damage to the jaw-secreting tissue, perhaps due to injury. The flexures that follow the growth lines probably represent pauses in growth due to stress, after which growth resumed, and are not related to injuries to the jaws.

The injuries on these jaws may be due to several factors. They may have been produced during feeding. In their natural habitat, nautilus regularly feed on crustaceans (Saunders and Ward, 1987; Saunders et al., 1987; Ward, 1987), as confirmed by reports of crustacean remains in the gut contents of freshly captured nautilus (Haven, 1972). In addition, Ward and Wicksten (1980) observed *Nautilus macromphalus* in captivity eating freshly molted exoskeletons of lobsters. Thus, the nautilus may have damaged their jaws by simply biting down on a hard crustacean carapace. Injuries may also have been caused by counterattacks of the prey. For example, Ward (1981) observed hermit crabs defending themselves against nautilus attack by breaking off pieces of the nautilus shell.

Alternatively, the injuries on nautilus jaws may have been produced by predators. The large breaks observed on nautilus shells have routinely been attributed to predators such as teleosts, sharks, and crabs (Arnold, 1985; Ward, 1987). There are few eye witness accounts of predatory attacks, but Saunders et al. (1987) observed such an attack by triggerfish on *Nautilus belauensis* in shallow water in Palau.

Another possible source of injuries on nautilus jaws may be linked to mating and courtship behavior. During copulation, a male nautilus grasps the shell of the female (Arnold, 1985, 1987), and the jaws of both sexes could be damaged in the process. The jaws of the male are especially vulnerable to counter attack by the female if the male is using its jaws to grasp the shell of the female. Injuries could also be produced during fights between males. Haven (1972) noted bites in the hoods and V-shaped breaks in the shells of *Nautilus pompilius* in captivity, which she attributed to combat between males. This behavior is consistent with the observation that in our sample of *N. macromphalus*, in which the distribution of sexes is known, jaw abnormalities are more common in males than females.

The location of the abnormalities sheds some light on the biology of nautilus. Nearly all of the abnormalities occur on the outer lamella of the lower jaw. Because the upper jaw is mostly covered by muscles and sits within the lower jaw, the outer lamella of the lower jaw is more vulnerable to injury. Furthermore, most of the abnormalities occur on the left side of the lower jaw. This pattern may be related to the position of the jaws in the shell. In males, the jaws are displaced toward the right side of the shell due to the

development of the spadix (Saunders and Spinosa, 1978; Saunders and Ward, 1987). Thus, during copulation, the apex of the jaws of the male lines up with the left side of the jaws of the female and, conversely, the apex of the jaws of the female lines up with the left side of the jaws of the male. This offset has also been cited to explain the disparity in the incidence of repaired shell breaks between the left and right sides of the shell. For example, Arnold (1985) noted that, in females, there is a higher incidence of injuries on the left side of the shell. The off-center position of the jaws in males also implies that, during male to male combat, the left side of the jaws is more vulnerable to damage than the right side.

The highest percentage of abnormalities occurs in *Nautilus belauensis*. This probably reflects the larger size of the jaws of this species. With more surface area to inspect, the probability of finding injuries is higher. In addition, studies of the longevity of nautilus suggest that *N. belauensis* is longer lived than the other nautilus species (Landman and Cochran, 1987). Because of their longer life span, these animals may have had a greater chance of sustaining injuries.

The paleontological implications of our observations bear on the arguments used to support the opercular theory of ammonite aptychi (Seilacher, 1993; Keupp, 2007). Traditionally, irregular marks on aptychi have been interpreted as healed injuries and, thus, proof of an opercular function. There are many illustrations of such marks on aptychi from the Jurassic of Germany (for example, Schindewolf, 1958: pls. 5, 9; Keupp et al., 1999: pl. 3, fig. 6; Keupp, 2000: 114, upper left; Engeser and Keupp, 2001: fig. 2). In addition, Landman et al. (2007: figs. 13.17–20) have illustrated such marks on the aptychi of *Baculites* from the Upper Cretaceous of North America.

Our study of abnormalities on nautilus jaws suggests that the formation of such features on aptychi may have been the result of the normal use of the jaws. However, we cannot exclude the possibility of an opercular function, although this interpretation requires more evidence. Alternatively, the aptychi may have simply served to strengthen the lower jaw. In this context, it is worth noting that nearly all of the abnormalities that we observed on nautilus jaws appear on the outside surface of the outer lamella of the lower jaw. Thus, the thick calcareous plates comprising the aptychus may have functioned to protect the outer surface of the lower jaw in ammonites, even if the aptychus did not rotate into a vertical position, as envisioned by Lehmann and Kulicki (1990).

FUTURE WORK

This is the first study of abnormalities on nautilus jaws (or any cephalopod jaws, for that matter). Further

studies could investigate the relationship between injuries on the nautilus shell and those on the jaws. Is an injury on the shell also expressed on the jaws? Such studies might provide additional insights into the ecology and behavior of nautilus—that is, their prey and their predators. It would also be interesting to determine if there are geographic differences in the occurrence of jaw injuries associated with different feeding habits.

From the paleontological point of view, our study suggests the need to more carefully examine the abnormalities on ammonite aptychi. Are these marks, in fact, the same as those on nautilus jaws? Do they appear on the inner and outer sides of the aptychus or only on the outer side? Do the injuries extend to the underlying chitinous layer of the jaw or are they restricted to the calcareous plates? The extent to which the marks on aptychi are the same as those on the jaws of nautilus will determine the extent to which our observations about nautilus can shed light on the functional interpretation of ammonite jaws.

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Effect of Temperature and Feeding Preference on Submerged Plants by the Island Apple Snail, *Pomacea insularum* (d'Orbigny, 1839) (Ampullariidae)

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Abstract. The island apple snail (*Pomacea insularum* (d'Orbigny, 1839)) is a South American snail that became naturalized in Florida waterways in the mid-1970s and has recently spread throughout much of the state. Food consumption by this herbivorous snail was determined in 10-day feeding trials at temperatures of 15 to 35°C. Optimum feeding of the exotic submerged plant *Hydrilla verticillata* (L.f.) Royle (hydrilla) occurred over a wide temperature range (20 to 35°C). However, snail growth was greatest at temperatures of 20 to 30°C. Free choice plant preference studies were conducted to determine feeding preferences for native and exotic submerged plants. One exotic and two native species (*H. verticillata*, *Najas guadalupensis* (Spreng.) Magnus (southern naiad) and *Chara* sp. (stonewort), respectively) were highly preferred by island apple snails, followed by the two native species *Potamogeton illinoensis* Morong. (Illinois pondweed) and *Vallisneria americana* Michx. (tapegrass). Leaves of the exotic species *Myriophyllum aquaticum* (Vell.) Verdc. (parrotsfeather) were eaten after the more preferred plants were consumed and no significant feeding was noted on the exotic species *Egeria densa* Planch. (Brazilian elodea). While island apple snails have distinct preferences for certain submerged plants, they consumed both native and exotic species, which may significantly affect growth of certain species and will likely change species composition of submerged plant communities in Florida wherever they are common.

Key Words: *canaliculata* complex, feeding preference, Florida waterways, invasive species, temperature effect.

INTRODUCTION

The island apple snail (*Pomacea insularum* (d'Orbigny, 1839)) is native to South and Central America and was most likely introduced into Florida through the aquarium trade (Thompson, 1997). Collections of this exotic snail have been reported sporadically in natural areas of Florida since 1978 (FLMNH, 2007), but recent reports suggest that the species has greatly expanded its range and has invaded virtually all counties in central and southern Florida (Denson, 2005). Specimens of *P. insularum* have been collected from a variety of habitats in Florida, including natural and constructed wetlands, streams, ponds, lakes and ditches that are inundated for most or all of the year. These habitats have earthen bottoms and are characterized by the presence of submerged, floating and/or emergent aquatic macrophytes. Areas frequented by *P. insularum* also typically have structures above the water line (e.g., emergent aquatic plants or man-made structures such as dikes or locks) onto which *P. insularum* deposits eggs.

There has been some confusion regarding the taxonomy of South American apple snails in Florida, but recent DNA studies indicated that the snails present in Florida (originally identified as *P. canaliculata* (Lamarck, 1822)) are actually *P. insularum*

(Rawlings et al., 2007). Field identification of species within the family *Pomacea* is challenging, since external characters are highly plastic and influenced by environmental factors. This is especially true of *P. haustorium* (Reeve, 1856) (titan), *P. canaliculata* (channeled) and *P. insularum* (island) apple snails, which are virtually indistinguishable from one another in morphology and behavior. In fact, these snails are so similar they are often grouped together into a “*canaliculata* complex.” Cazzaniga (2002) stated that all *canaliculata*-like apple snails may constitute a single, highly variable species and further noted that any *canaliculata*-like apple snail has the potential to become a pest and cause damage to aquatic ecosystems. *Canaliculata*-like apple snails can become quite large, but *P. insularum* is considered the largest of the group and can attain a shell height of up to 150 mm (Benson, 2008; Gettys and Haller, 2007).

One factor that influences the feeding of *canaliculata*-like apple snails is temperature. Estebenet and Cazzaniga (1992) and Estebenet and Martin (2002) found that *P. canaliculata* grew most quickly under warm conditions (>25°C) and stopped feeding during cool temperatures (e.g., <18°C). These results suggest that the warm year-round temperatures found throughout much of Florida may provide an ideal habitat for *P. insularum*; therefore, the first objective of this experi-

ment was to measure the effect of temperature on consumption of *Hydrilla verticillata* (L.f.) Royle (hydrilla), an aquatic weed that is ubiquitous in aquatic systems throughout Florida, Texas and other regions that have been invaded by *P. insularum*.

Canaliculata-like snails in the genus *Pomacea* are voracious herbivores and have been introduced to some parts of the world as biocontrol measures to manage aquatic weeds (Cowie, 2002; Okuma et al., 1994; Wada, 1997). Some workers have reported that *canaliculata*-like apple snails actively select their food and exhibit a preference for some plant material. For example, Fukushima et al. (2001) found that *P. canaliculata* preferred most fruits and vegetables to rice seedlings. Lach et al. (2000) stated that *P. canaliculata* selected *Vigna marina* (Burm.) Merr. (beach pea or notched cowpea) over *Eichhornia crassipes* (Mart.) Solms (waterhyacinth), *Ludwigia octovalvis* (Jacq.) P.H. Raven. (primrose willow) and *Pistia stratiotes* L. (water-lettuce). Carlsson and Lacoursiere (2005) stated that *P. canaliculata* virtually eliminated *Lemna minor* L. (duckweed) and *E. crassipes* after 6 and 21 days of grazing, respectively, but reduced the biomass of *Ipomea aquatica* Forsk. (waterspinach) by only 20% after 32 days of grazing. Estebenet (1995) found that *P. canaliculata* preferred *Zannichellia palustris* L. (horned pondweed) over *Myriophyllum elatinoides* Gaudin (water milfoil or Christmas-tree plant) and *Chara contraria* A. Braun ex Kutz. (opposite stonewort); snails had a low preference for *Rorippa nasturtium-aquaticum* [L.] Hayek (watercress) and *Potamogeton striatus* Ruiz & Pavón (broadleaf pondweed) and did not select *Elodea canadensis* LC Rich. in Michx. (common waterweed). In contrast, Cazzaniga and Estebenet (1984) and Cowie (2002) suggested that these snails feed indiscriminately on virtually anything, including algae, macrophytes, phytoplankton, detritus and even immature snails of other species. In addition, Peltzer and Lajmanovich (2003) reported that *Hyla pulchella* Duméril & Bibron, 1841 (anuran tadpoles) were consumed by juvenile *P. canaliculata*. A variety of submerged macrophytes species are found in Florida; some species are native, while others are exotic and invasive. Common native aquatic macrophytes in Florida include *Vallisneria americana* Michx. (tape-grass), *Najas guadalupensis* (Spreng.) Magnus (southern naiad), *Potamogeton illinoensis* Morong. (Illinois pondweed), and *Chara* sp. (stonewort). Invasive exotic species common in Florida waters include *H. verticillata* (native to Asia, Africa and Australia), along with the South American natives *Egeria densa* Planch. (Brazilian elodea) and *Myriophyllum aquaticum* (Vell.) Verdc. (parrotfeather). Native species of macrophytes are more desirable than exotic species, but many aquatic fauna that rely on submerged vegetation as a habitat for nesting and spawning do not discriminate

between native and exotic species. If the *canaliculata*-like *P. insularum* indiscriminately consumes all flora, the consequences to Florida's ecosystem could be devastating since the snail can cause significant changes to wetland ecosystems through herbivory of aquatic macrophytes. High densities of *P. canaliculata* in natural wetlands in Thailand caused an almost complete loss of aquatic macrophytes through grazing (Carlsson et al., 2004). Wetlands in central and south Florida persist under the same environmental conditions as those in Thailand, so it is reasonable to expect the same situation to occur if waterways in Florida become infested with *P. insularum*. Data regarding the feeding habits and macrophyte preferences of *canaliculata*-like apple snails are conflicting and there are no reports that address the feeding habits of snails positively identified as *P. insularum*; therefore, the second objective of this study was to determine if *P. insularum* is truly a non-specific feeder or if the snail shows a feeding preference when presented with a diversity of native and exotic submerged macrophytes commonly found in Florida waterways.

MATERIALS AND METHODS

Several hundred specimens of *P. insularum* were collected from a heavily infested earthen irrigation pond (surface area 0.12 ha; maximum depth 1 m) at a wholesale aquatic plant nursery in Lake City, Florida. Snails were maintained in a covered greenhouse (ambient temperature $28 \pm 3^\circ\text{C}$) at the University of Florida's Center for Aquatic and Invasive Plants in Gainesville, FL for 2 to 3 weeks prior to their utilization in these experiments. Each snail was measured (height and width), weighed and assigned a letter/number combination code using the following system. Snails were assigned one of six letter classes based on weight (A: <25 g; B: 25 to 35 g; C: 35.1 to 45 g; D: 45.1 to 55 g; E: 55.1 to 65 g; and F: >75 g) and were numbered in ascending order (e.g., snail D6 weighed between 45.1 and 55 g and was the 6th snail labeled in weight class D). The shell of each snail was gently cleaned and dried using a disposable paper towel, then the alphanumeric code was painted onto the snail shell using nail polish so that snails could easily be identified. This coding system allowed positive identification of each snail and was used to ensure that each snail was only used in a single study.

Effect of Temperature on Consumption

The objective of this study was to measure the effect of temperature on consumption of macrophytes by *P. insularum*. The macrophyte *H. verticillata* was used in this study because it is an exotic species that is ubiquitous in aquatic systems throughout Florida,

Texas and other regions that have been invaded by *P. insularum*. The temperature regimes in this study were chosen to represent the range of seasonal variation in water temperature in Florida. Consumption of *H. verticillata* under five temperature regimes (15°C, 20°C, 25°C, 30°C and 35°C) was investigated in growth chambers (Percival model E36L, Perry, IA). Digital controls on the chambers were programmed to maintain a daylength of 14 hr and to hold water temperature at the target temperature $\pm 0.5^\circ\text{C}$. Four 5-gallon aquaria were placed in each growth chamber. Water was maintained at a depth of ca. 25 cm to provide a water volume of ca. 12 L and aeration was supplied by a standard aquarium aerator. Snails were selected for uniform weight and one snail was placed in each filled aquarium within the growth chamber. Water temperature was adjusted by 3°C per day to reduce shock during the transition from ambient greenhouse temperature ($28 \pm 3^\circ\text{C}$) to the assigned experimental temperature regime. Snails were acclimatized to experimental temperatures for 2, 4 or 6 d for 25°C and 30°C treatments, 20°C and 35°C treatments and 15°C treatment, respectively, and were fed *H. verticillata* ad libitum during acclimatization. Snails were starved for 24 hr after acclimatization and were weighed prior to commencement of each study. Each study lasted 10 d and each snail was offered a total of 90 g of *H. verticillata* during each study (30 g each on days 1, 4 and 7). Water in the aquaria quickly became fouled with feces and detritus, so additional aquaria were filled with water and placed in each growth chamber on days 3 and 6. Snails, aerators and uneaten *H. verticillata* were moved to these clean, acclimatized tanks on days 4 and 7. Total biomass consumption was calculated by weighing uneaten plant material remaining in each aquarium on day 10 of each study and snails were weighed on day 10 as well. Data were analyzed to detect differences in plant biomass consumption and differences in snail weight under each temperature regime.

Feeding Preference

Macrophytes were maintained in a greenhouse under natural daylength during Fall 2005 at the University of Florida's Center for Aquatic and Invasive Plants in Gainesville, FL. All macrophytes were grown in square pots (10 cm square \times 12 cm deep) filled with 1 kg of coarse builder's sand amended with 1 g of Osmocote® Plus 15-8-12 controlled-release fertilizer (The Scotts Co. LLC, Marysville OH). Seven submerged macrophytes – *H. verticillata*, *V. americana*, *E. densa*, *N. guadalupensis*, *P. illinoensis*, *Chara* sp. and *M. aquaticum* – were utilized in this experiment to represent some of the most common native and exotic aquatic species found in Florida waters. Macrophytes were propagated by

vegetative means with either four 10-cm-long apical cuttings per pot (*H. verticillata*, *E. densa*, *N. guadalupensis*, *P. illinoensis* and *M. aquaticum*), one clump of ten 10-cm-long apical cuttings per pot (*Chara* sp.) or three rooted plantlets per pot (*V. americana*). These propagation methods were used because our preliminary studies suggested these protocols would supply snails with sufficient amounts of each macrophyte species. Macrophytes were propagated 7 to 14 d prior to commencement of the experiment and were grown in circular fiberglass tanks (inside diameter 105 cm, water depth 55 cm) filled with well water to a volume of ca. 475 L (pH 8, temperature range ca. 22°C to 32°C).

All food was withheld from snails for 48 hr prior to commencement of the food preference experiments. Naylor (1996) stated that a density of 8 snails/m² (32,376 snails/acre) could reduce rice yields by 90%, and snail densities in our experiment bracket that of Naylor (12 snails/m² = 46,729/acre in Study 1 and 7 snails/m² = 28,037/acre in Study 2). Snails were sorted by weight and then randomly allocated to each tank so that all treatment tanks had similar amounts of snail biomass (i.e., mean weights of 658.7 ± 9.2 g and 407.7 ± 7.1 g in Studies 1 and 2, respectively). Shell height of snails used in these experiments ranged from 58 to 74 mm, and biomass per snail ranged from 50 to 86 g.

Eight circular fiberglass tanks (inside diameter 105 cm, water depth 55 cm) were used in this experiment with 4 pots of each macrophyte species placed in a completely randomized design in each tank. Four tanks were used as controls and contained only macrophytes, while the remaining four tanks were populated with macrophytes and *P. insularum*. All tanks were covered with fiberglass insect screening to ensure containment of the snails in treatment tanks and to maintain consistent light conditions between snail tanks and control tanks. Feeding preference data were collected every other day (Study 1) or every third day (Study 2). One pot of each macrophyte species was randomly removed from each tank at each data collection interval, resulting in four replicates of each treatment (control vs. snails). This allowed us to account for macrophyte growth during the course of the each study. Two replicates of this experiment were conducted in Fall 2005. Study 1 ran from 22 Sept. to 30 Sept. and Study 2 ran from 24 Oct. to 2 Nov. Experimental parameters were similar in both studies except for snail density (10 snails per tank in Study 1 and 6 snails per tank in Study 2) and macrophyte removal interval (2, 4, 6 and 8 d in Study 1 and 3, 6, 9 and 12 d in Study 2). Snails consumed macrophytes more quickly than anticipated in Study 1, so snail density and macrophyte removal interval for Study 2 were modified in an attempt to more clearly identify the snails' preference among the macrophytes offered. Separate analyses were performed for each study to

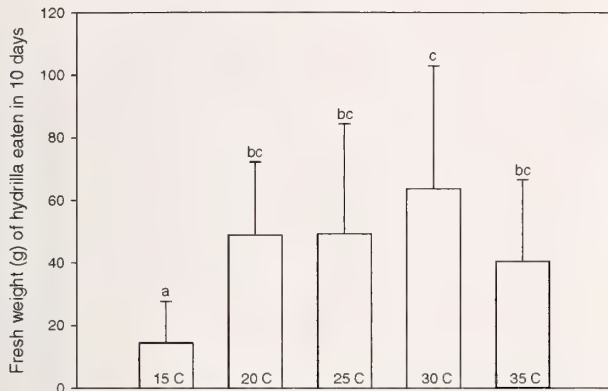


Figure 1. Amount of *H. verticillata* eaten by *P. insularum* under various temperature regimes. Each bar represents the mean of four replicates (snails) per temperature regime and temperature regimes coded with the same letter indicates that *H. verticillata* consumption was not significantly different at $P = 0.05$.

account for seasonal differences in plant growth. Each study was treated as a factorial ($2 \times 7 \times 4$) design, with 2 treatments (snails vs. control), 7 macrophyte species and 4 macrophyte removal intervals. Macrophyte shoot material was weighed to determine fresh weights for all treatments and percent macrophyte material eaten by snails was then calculated by comparing uneaten macrophyte weight of each species in snail tanks to the mean of the same macrophyte species in control tanks. Direct consumption data were not analyzed because macrophyte biomass varied by species (e.g., three rooted plantlets of *V. americana* weigh considerably more than ten 10-cm-long apical cuttings of *Chara* sp.), so the use of percentage data allowed us to standardize consumption across macrophytes of disparate biomass. These percentage data were subjected to analyses of variance (SAS Version 9.1, SAS Institute Inc., Cary, NC, USA) to detect differences between treated and control plants of the same species and differences among plant species harvested at a given time interval.

RESULTS

Effect of Temperature on Herbivory

Snails consumed less plant material at 15°C than at intermediate and high temperatures (20°C, 25°C, 30°C and 35°C) (Figure 1). Also, snails grew faster at intermediate temperatures (20°C, 25°C and 30°C) than at low and high temperatures (15°C and 35°C) (Figure 2). Snails held at 30°C consumed an average of 63.8 g of *H. verticillata* over the course of the study (a daily average of 10.0 g of *H. verticillata* per kg of snail weight) (Figure 1) and gained an average of 2.3 g of biomass over the course of the 10-day study period

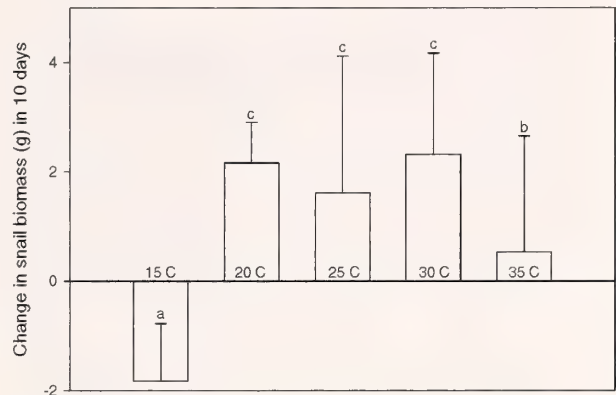


Figure 2. Change in biomass of *P. insularum* under various temperature regimes. Each bar represents the mean of four replicates (snails) per temperature regime and temperature regimes coded with the same letter are not significantly different at $P = 0.05$.

(Figure 2). In contrast, snails kept at 15°C ate an average of 14.5 g of *H. verticillata* during the course of the study (a daily average of 2.3 g of *H. verticillata* per kg of snail biomass) (Figure 1) and actually lost an average of 1.8 g of body weight during the 10-day study period (Figure 2). These results indicate that optimum consumption of the submerged plant *H. verticillata* by *P. insularum* occurred over a wide temperature range (20 to 35°C). However, snail growth was greatest at temperatures of 20 to 30°C.

Feeding Preference

Snail weight did not change significantly during the course of Study 1, as final mean biomass per tank was 655.8 ± 5.7 g. Snails in Study 1 preferred *N. guadalupensis*, *Chara* sp. and *H. verticillata* to *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa*; with no difference noted among *N. guadalupensis*, *Chara* sp. and *H. verticillata* at any sampling interval (Figure 3a). Snails ate 89.5%, 82.4% and 75.2% of *N. guadalupensis*, *Chara* sp. and *H. verticillata*, respectively, within two days of commencement of the study and had consumed 100% of these species by the fourth day of Study 1 (Figure 3a). Snails selected *P. illinoensis* and *V. americana* over *M. aquaticum* and *E. densa* when most-preferred macrophytes were depleted. Snails consumed *M. aquaticum* when most-preferred and less-preferred macrophyte species were depleted, but typically fed on leaves and not stem material. Fresh biomass of *E. densa* in snail tanks was not different from that in control tanks at the conclusion of the study; therefore, *E. densa* was not eaten by snails, even when all other plant material had been consumed. Most-preferred macrophytes in Study 1 were *N. guadalupensis*, *Chara* sp. and *H. verticillata*. Less-preferred macrophytes *P. illinoensis* and *V. americana*

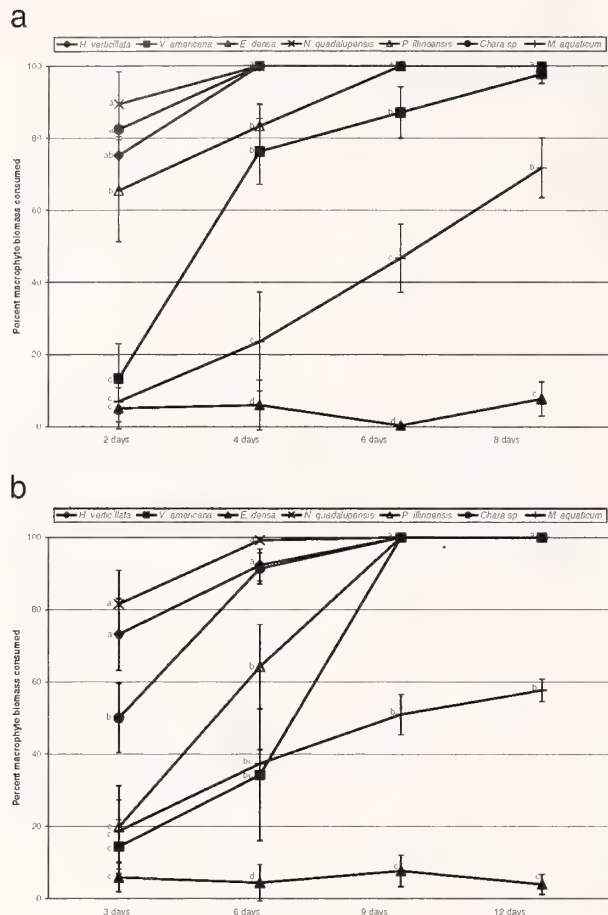


Figure 3a. Percent macrophyte biomass eaten by *P. insularum* during Study 1. Each point represents the mean of four replicates per species and species coded with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard error.

Figure 3b. Percent macrophyte biomass eaten by *P. insularum* during Study 2. Each point represents the mean of four replicates per species and species coded with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard error.

were consumed when most-preferred macrophytes were depleted, and least-preferred macrophytes (with little or no feeding damage) were *M. aquaticum* and *E. densa*.

Snail weight did not change significantly during Study 2, as final mean biomass per tank was 410.3 ± 8.0 g. Snails in Study 2 preferred *N. guadalupensis* and *H. verticillata* to *Chara sp.*, *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa*, with no difference noted between *N. guadalupensis* and *H. verticillata* at any sampling interval (Figure 3b). Snails ate 81.5% and 73.2% of the *N. guadalupensis* and *H. verticillata*, respectively, within three days of commencement of the study. Snails preferred *Chara sp.* to *P. illinoensis*, *V. americana*, *M. aquaticum* and *E. densa* and consumed 50.0% of *Chara sp.* by the third day of Study 2

(Figure 3b). There was no difference in consumption of *N. guadalupensis*, *H. verticillata* and *Chara sp.* by the sixth day of Study 2 because nearly all macrophyte material of these most-preferred species was consumed prior to day 6 (Figure 3b). Snails selected *P. illinoensis* over *V. americana*, *M. aquaticum* and *E. densa* when most-preferred macrophytes were depleted and consumed *V. americana* in preference to *M. aquaticum* and *E. densa* when most-preferred macrophytes and *P. illinoensis* were scarce. As in Study 1, snails fed on leaves of *M. aquaticum* when preferred species were scarce and *E. densa* was not eaten by snails even when all other macrophyte material had been consumed. Most-preferred macrophytes in Study 2 were *N. guadalupensis* and *H. verticillata*. The less-preferred macrophyte *Chara sp.* was selected over *P. illinoensis* and *V. americana*, and least-preferred macrophytes (with little or no feeding damage) were *M. aquaticum* and *E. densa*.

DISCUSSION

This research revealed that *P. insularum* consumed the greatest amount of macrophyte biomass and accumulated the greatest amount of body weight when exposed to moderate temperatures (i.e., 20°C to 30°C). This finding does not bode well for Florida's wetlands and waterways, since water temperature falls in this range throughout most of the year in central and southern Florida. These results also showed that *P. insularum* does indeed exhibit a feeding preference if offered an assortment of submerged macrophytes over a short time interval. However, it is unlikely that macrophyte origin plays a role in *P. insularum*'s food selection, since both native (*N. guadalupensis*) and exotic (*H. verticillata*) species were preferred in both studies. Three macrophyte species (including the weed *H. verticillata*) were most preferred, while *E. densa* was completely rejected by snails in this experiment, even when the majority of other macrophyte material had been consumed. It is interesting to note that *H. verticillata* (native to Africa or Asia and strongly preferred by *P. insularum*) and *E. densa* (native to South America and rejected by *P. insularum*) are both members of the Hydrocharitaceae, as is *Elodea canadensis* LC Rich. in Michx (common waterweed). Other researchers (e.g., Carlsson and Lacoursiere, 2005; Estebenet, 1995) have noted that *P. canaliculata* will not eat *E. canadensis*, which is native to temperate regions of North America; in fact, snails offered only *E. canadensis* by Estebenet (1995) refused to eat the macrophyte and eventually starved to death. These three species are submerged macrophytes that are morphologically similar and difficult to distinguish from one another, so the reason for the snails' preference for *H. verticillata* and rejection of *E. densa* and *E. canadensis* is unclear.

It is commonly thought that macrophytes employ structural defenses (e.g., spines, thorns or toughness) to deter feeding by herbivores. Pennings and Paul (1992) found that plant toughness and calcification deterred feeding by the marine gastropod *Dolabella auricularia* (Lightfoot, 1786) (sea-hare). However, *D. auricularia* is able to sequester plant secondary metabolites that may act as chemical feeding deterrents in other herbivorous species. Chemical defenses against herbivory have been extensively studied in terrestrial plants but have only recently gained attention in aquatic macrophytes. Secondary metabolites including alkaloids, glucosinates, polyphenols and flavonols have been identified in a number of aquatic macrophytes and reduce or prevent consumption by herbivores. Erhard et al. (2007) found that flavonoids and other allelochemicals produced by *Elodea nuttallii* (Planch.) St. John (western waterweed) reduced feeding by the larvae of the generalist pyralid aquatic moth *Acentria ephemerella* (Lepidoptera, Pyralidae). Herbivory by *Procambarus clarkii* (Girard, 1852) (red swamp crayfish) was depressed in *Habenaria repens* Nutt. (aquatic orchid) by an endogenous ester (Wilson et al., 1999) and in *Saururus cernuus* L. (lizards-tail) by an array of lignoid metabolites (Kubanek et al., 2001). *Rorippa nasturtium-aquaticum* (L.) Hayek (syn. *Nasturtium officinale*) (watercress) is protected by 2-phenylethyl isothiocyanate, a chemical synthesized by the endogenous glucosinolate-myrosinase system and highly toxic to freshwater gastropods in the genus *Physella* (Kerfoot et al., 1998; Newman et al., 1992). It is unknown whether *E. densa* used in our experiment utilizes chemical defenses such as these to prevent or reduce herbivory; however, the leaf structure and morphology of *E. densa* (rejected by *P. insularum*) are similar to that of the closely related and most-preferred *H. verticillata*, so it is unlikely that structural defenses were responsible for *P. insularum*'s rejection of *E. densa*. It is possible that *E. densa* possesses a chemically based feeding deterrent system to deter herbivory by *P. insularum*. While this question is beyond the scope of our experiment, it certainly merits further investigation.

The majority of studies investigating the impact of herbivory by species of *Pomacea* have focused on *P. canaliculata* (channeled apple snail), the type species for the "*canaliculata* complex" of which *P. insularum* is a member. Cazzaniga (2002) suggested that any *canaliculata*-like apple snail had the potential to become a pest and cause damage to aquatic ecosystems, so it is likely that the field behavior of *P. insularum* will be similar to that reported for *P. canaliculata*. Snails belonging to the *canaliculata* complex have been introduced to other parts of the world as biocontrol agents to manage aquatic weeds (Cowie, 2002; Okuma et al., 1994; Wada, 1997). For example, Perera and Walls (1996) found that *P. canaliculata* effectively

controlled *Pistia stratiotes* L. (water lettuce) in the Caribbean. Unfortunately, the snails also feed on native plants, resulting in detrimental effects to the native fauna that rely on endemic plants for food and shelter (Simberloff and Stiling, 1996). Field experiments by Carlsson et al. (2004) revealed that *P. canaliculata* consumed most aquatic vegetation and caused bodies of water to become turbid with a dominance of planktonic algae. These workers also found that densities of >2 snails per m² in some of Thailand's natural wetlands resulted in a shift in ecosystem state and function – virtually all aquatic plants were eaten and serious increases were recorded in nutrient concentrations and phytoplankton biomass (Carlsson et al., 2004). Herbivory by *P. canaliculata* extends to commercially cultivated crops as well; in fact, a density of 8 snails per m² can reduce yields by 90% in *Oryza sativa* L. (rice) (Naylor, 1996). Population densities of *P. insularum*-infested wetlands and flooded agricultural sites are often unavailable, but even small populations can explode quickly since *canaliculata*-type snails are highly fecund (Martin and Estebenet, 2002; Tanaka et al., 1999; Teo, 2004). Based on these reports and the results of our experiments, it is likely that wetland areas infested with *P. insularum* will experience severe damage similar to that reported by Carlsson et al. (2004). Also, drastically reduced yields should be expected in inundated agricultural crops (e.g., *O. sativa*, *Colocasia esculenta* (L.) Schott (taro)) grown in areas like Texas, Louisiana, Florida and Hawaii.

These experiments provide additional documentation regarding the feeding habits of *P. insularum* and the positive influence of moderate temperatures on herbivory and growth of the species. It is unlikely that macrophyte origin plays a role in *P. insularum*'s food selection, so special precautions must be followed to exclude this snail from ecosystems where aquatic macrophytes could be decimated by its presence. Many aquatic fauna rely on submerged vegetation as a habitat for nesting and spawning, so *P. insularum*'s indiscriminate consumption of aquatic macrophytes would have devastating consequences to Florida's ecosystem. Other countries have attempted to use *canaliculata*-type snails to control nuisance aquatic plants, but their indiscriminate feeding habits have eliminated virtually all aquatic vegetation. Most aquatic systems support a variety of herbivores, but these species rarely feed at a level that significantly impacts macrophyte populations. Therefore, it is critically important that *P. insularum* and other *canaliculata*-type snails be excluded or eradicated in Florida and in other states at risk to prevent the decimation of critical aquatic ecosystems. Additional research should be conducted to assess the impact of *P. insularum* on other aquatic macrophytes, including floating, emergent and other submerged species. Of

particular interest would be predictive studies to determine the impact of population density of *P. insularum* on aquatic ecosystems.

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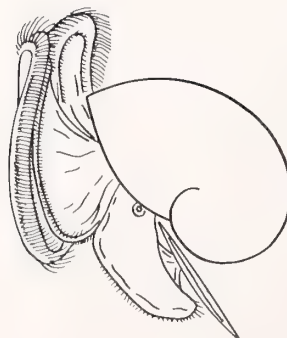
CONTENTS — *Continued*

New Genera and Species of Peristerniinae (Gastropoda: Fascioliidae) from the Caribbean Region, with Comments on the Fascioliid Fauna of Bermuda WILLIAM G. LYONS AND MARTIN AVERY SNYDER	225
Injuries on Nautilus Jaws: Implications for the Function of Ammonite Aptychi ISABELLE KRUTA AND NEIL H. LANDMAN	241
Effect of Temperature and Feeding Preference on Submerged Plants by the Island Apple Snail, <i>Pomacea insularum</i> (d'Orbigny, 1839) (Ampullariidae) L. A. GETTYS, W. T. HALLER, C. R. MUDGE AND T. J. KOSCHNICK	248

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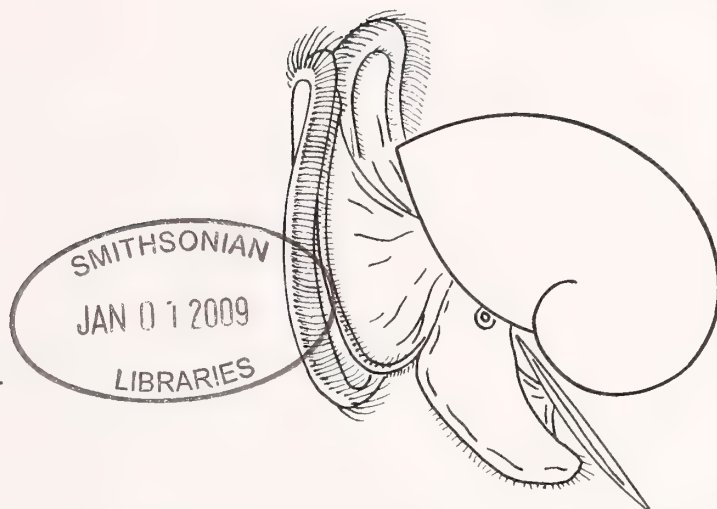


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CONTENTS

- A New Genus for *Vesicomya inflata* Kanie and Nishida, a Lucinid Shell Convergent with that of Vesicomys, from Cretaceous Strata of Hokkaido, Japan
KAZUTAKA AMANO, ROBERT G. JENKINS, YUKITO KURIHARA AND STEFFEN KIEL 255
- A Quantitative Assessment of Spermatozoan Morphology in *Nutricula confusa* and *Nutricula tantilla* (Bivalvia: Veneridae).
JAMES GERAGHTY, MICHAEL P. RUSSELL AND NORMAN DOLLAHON 263
- Effects of Estivation on the Concentrations of Selected Carboxylic Acids of Two Strains of *Helisoma trivolvis*
MARK A. BROWN, MICHAEL J. CHEJLAVA, BERNARD FRIED, AND JOSEPH SHERMA 269
- Cenozoic *Nacella* (Patellogastropoda: Nacellidae) from Peru and Chile: Filling in the Gaps
THOMAS J. DEVRIES 274
- A New Species of *Fissurella* from São Pedro e São Paulo Archipelago, Brazil (Vetigastropoda, Fissurellidae)
LUIZ RICARDO L. SIMONE 292
- The Gastropod *Spiricella* (Opisthobranchia: Umbraculidae) in the Recent Caribbean: A truly unexpected finding!
CARLOS MARQUES DA SILVA & BERNARD M. LANDAU 305
- Functional Anatomy of *Bankia fimbriatula* Moll & Roch, 1931 (Bivalvia: Teredinidae)
MARIA JÚLIA MARTINS-SILVA AND WALTER NARCHI 309

CONTENTS — Continued

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A New Genus for *Vesicomya inflata* Kanie & Nishida, a Lucinid Shell Convergent with that of Vesicomyids, from Cretaceous Strata of Hokkaido, Japan

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Abstract. Newly collected specimens of the large bivalve *Vesicomya inflata* Kanie & Nishida from the lower Cenomanian Tenkaritoge Formation reveal that it is not a vesicomyid but is instead an unusual lucinid. The new monotypic genus *Ezolucina* is herein proposed for this species, which is characterized by venerid or vesicomyid shell shape, large size, a smooth surface, a deeply impressed lunule, one cardinal and one anterior lateral tooth in the right valve, and two cardinal teeth in the left valve. Stable carbon isotope analyses and petrographic observations show that the carbonate concretions yielding this species do not represent ancient hydrocarbon-seep deposits as was suggested previously. Rather, *Ezolucina inflata* and the associated solemyid, lucinid, thyasirid, and manzanellid bivalves lived in organic- and sulfide-rich sediment.

INTRODUCTION

Large fossil bivalves from the “Middle Yezo Group” in northern Hokkaido, Japan, were described by Kanie & Nishida (2000) as *Vesicomya inflata*, and listed as being the earliest record for the genus *Vesicomya* (Campbell, 2006; Kiel & Little, 2006). They were found in two large calcareous concretions surrounded by mudstone, and were associated with the solemyid *Acharax cretacea* Kanie & Nishida, 2000 and the lucinid *Miltha* sp. Extant members of these bivalve taxa harbor chemoautotrophic endosymbionts, and because carbonate concretions bearing these taxa have repeatedly been demonstrated to represent ancient hydrocarbon-seep deposits (Majima et al., 2005; Campbell, 2006), the concretions bearing *Vesicomya inflata* were interpreted as ancient hydrocarbon-seep deposits (Kanie & Nishida, 2000; Kanie et al., 2000).

Living *Vesicomya* species have small shells that rarely exceed 13 mm in length (Cosel & Salas, 2001)

and belong to a clade informally known as “small” vesicomyids, composed of the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon*, *Callogonia* and *Pliocardia* (cf. Cosel & Salas, 2001; Krylova & Sahling, 2006). In contrast, the Cretaceous “*Vesicomya*” *inflata* reaches a length of up to 157 mm. In a recent revision of fossil North Pacific vesicomyids, Amano & Kiel (2007) pointed out that *V. inflata* has a deeply impressed asymmetrical lunule, a feature unknown in vesicomyids, and that its hinge structure had neither been described nor illustrated. Consequently, Amano & Kiel (2007) excluded *V. inflata* from the Vesicomyidae and suggested lucinid affinities instead.

Newly collected specimens from the type locality of “*Vesicomya*” *inflata* at Sanjussen-zawa Creek in northern Hokkaido possess hinge dentition, a pallial line, and adductor scars that clearly place this species in a new genus of the Lucinidae. In addition, petrographic thin sections and stable carbon isotope analyses of the fossil-bearing concretions are used to evaluate the

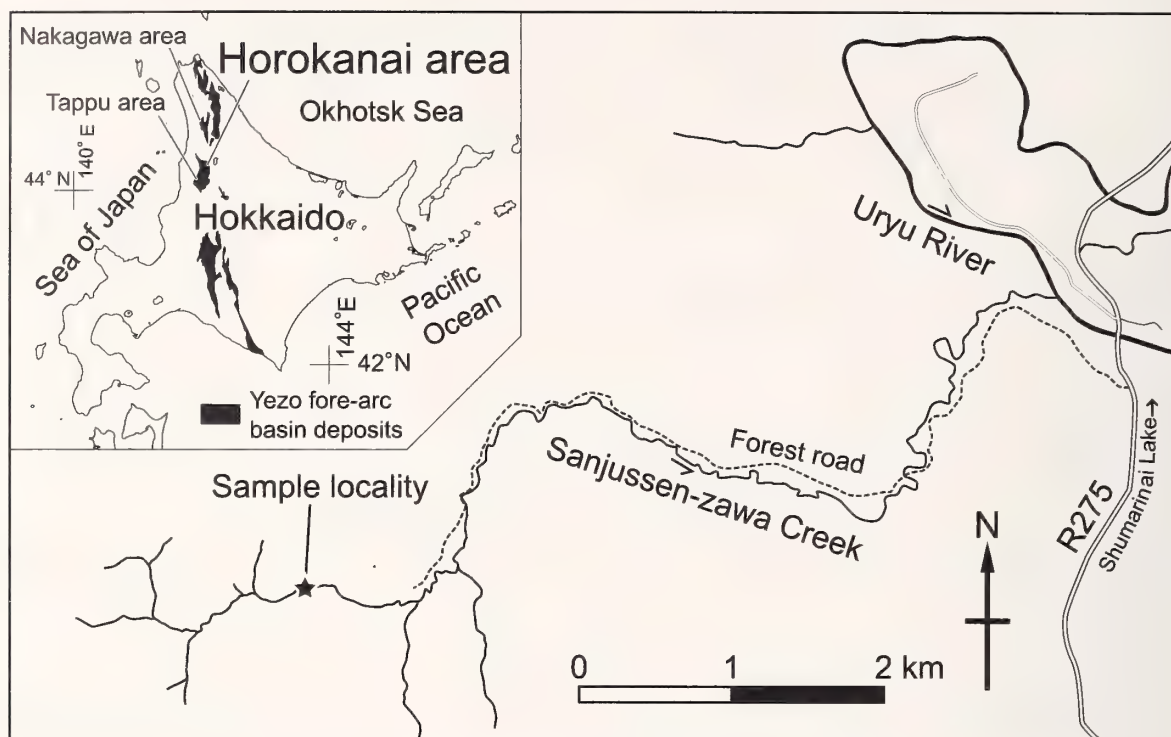


Figure 1. Type locality of *Ezolucina inflata* (Kanie & Nishida).

environmental reconstruction of this site as an ancient hydrocarbon seep.

MATERIALS AND METHODS

The type material was examined at the Yokosuka City Museum, and nine new specimens of “*Vesicomya*” *inflata* were collected from four float carbonate concretions with molluscan fossils (HRK A–D) at the type locality in northern Hokkaido (Figure 1). Stratigraphically the specimens are from the My 4 Member of the Tenkaritoge Formation, which is considered early Cenomanian (Hashimoto et al., 1965; Nishida et al., 1998). The figured specimens and additional new material are housed at the Joetsu University of Education (JUE).

The mineralogy of the fossil-bearing concretions was identified by thin-section observations and X-ray diffraction (XRD) analysis. Standard thin-section observations were performed by plane- and cross-polarized and reflected light microscopy. XRD analyses were carried out on unoriented slurries using a PANalytical X’Pert PRO at the Department of Earth and Planetary Science, the University of Tokyo (EPUT). Carbon and oxygen isotopes were analyzed using 2 to 10 mg powdered carbonate matrix. Carbon dioxide was produced from each powdered sample by reaction with 100% phosphoric acid in vacuo (25°C), and analyzed with a Finnigan MAT252 mass spec-

trometer at EPUT. Carbon isotopic composition is expressed in the conventional δ notation relative to the Vienna Pee Dee Belemnite standard ($\delta^{13}\text{C}$, ‰ vs. V-PDB, standard deviation <0.03‰).

MINERALOGY AND ISOTOPE COMPOSITION OF CARBONATES

Thin-section observation and XRD analysis show that the concretions are almost entirely composed of homogeneous micritic calcite and siliciclastic sediment. Structures typical for methane-induced carbonates, like clotted fabrics and stromatolitic laminae (cf. Greinert et al., 2002; Peckmann & Thiel, 2004), were not seen. $\delta^{13}\text{C}$ values range from -7.7 to -6.3 ‰ (vs. V-PDB)

Table 1

Stable carbon and oxygen isotope composition of the carbonate concretions from the type locality of *Ezolucina inflata* (Kanie & Nishida).

Sample no.	Texture	Mineralogy	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
HRK A	micrite	calcite	-7.4	-1.3
HRK A	micrite	calcite	-7.3	-1.2
HRK B	micrite	calcite	-6.3	-3.8
HRK C	micrite	calcite	-6.7	-4.9
HRK C	micrite	calcite	-6.5	-4.2
HRK C	micrite	calcite	-7.7	-5.2

(Table 1) and are also not indicative of anaerobic methane oxidation. Methane-derived carbonate usually shows $\delta^{13}\text{C}$ values lower than -40‰ (cf. Peckmann & Thiel, 2004). Thus, neither thin section observations nor stable isotope analyses support the idea of Kanie & Nishida (2000) and Kanie et al. (2000) that “*Vesicomya*” *inflata* and associated mollusks lived at an ancient hydrocarbon seep.

SYSTEMATICS

Family Lucinidae Fleming, 1828

Genus *Ezolucina* Amano, Jenkins, Kurihara & Kiel, gen. nov.

Type species: *Vesicomya inflata* Kanie & Nishida, 2000.

Diagnosis: Large, inflated veneriform shell with smooth surface except for rough, low commarginal lamellae; posterior radial sulcus weak, and lunule deeply impressed. Hinge of right valve with one stout cardinal tooth and an anterior lateral tooth, left valve hinge with two cardinal teeth. Anterior adductor scar quadrate and anteriorly detached from pallial line; pallial line entire and deeply impressed.

Discussion: Here Gabb, 1866 is similar to *Ezolucina* gen. nov. by having one cardinal tooth, one anterior lateral tooth in right valve and a deeply impressed lunule, but differs from *Ezolucina* by its smaller shell with fine ventral crenulations, and its much more deeply impressed lunule. Another large Cretaceous lucinid is *Nipponothracia*, which differs from *Ezolucina* by having an edentulous hinge and a very elongate anterior adductor scar (cf. Kanie & Sakai, 1997; Kase et al., 2007; Kiel et al., 2008). The medium-sized North American lucinid *Nymphalucina* Speden, 1970 from the Late Cretaceous Pierre Shale and Fox Hill Formation is oval in shape and lacks the sloping posterodorsal margin of *Ezolucina*. *Trinitasia* Maury, 1928, which was questionably placed in Lucinidae by Chavan (1969), is comparable in shell form and sculpture, but based on internal shell features Woodring (1982) showed that *Trinitasia* is not a lucinid but a mactrid.

Etymology: A combination of the old name of Hokkaido (Ezo) and the genus *Lucina*.

Ezolucina inflata (Kanie & Nishida, 2000)

(Figures 2–9)

Vesicomya inflata Kanie & Nishida, 2000: p. 79–82, .figs. 1, 2.

Holotype: Articulated specimen, length 131.8 mm, height 105.4 mm, width 76.3 mm, YCM-GP1173.

Paratype: Articulated specimen, length 82.6 mm+, height 59.8 mm, width 35.8 mm+, YCM-GP1174.

Topotypes: Articulated specimen, length 157.5 mm, height 123.8 mm, width 74.0 mm+, YCM-GP1177; right valve, length 33.7 mm, height 26.2 mm, JUE no. 15853; right valve, length 28.9 mm, height 21.9 mm, JUE no. 15854; articulated specimen, length 15.4 mm, height 13.5 mm, width 5.9 mm, JUE no. 15855.

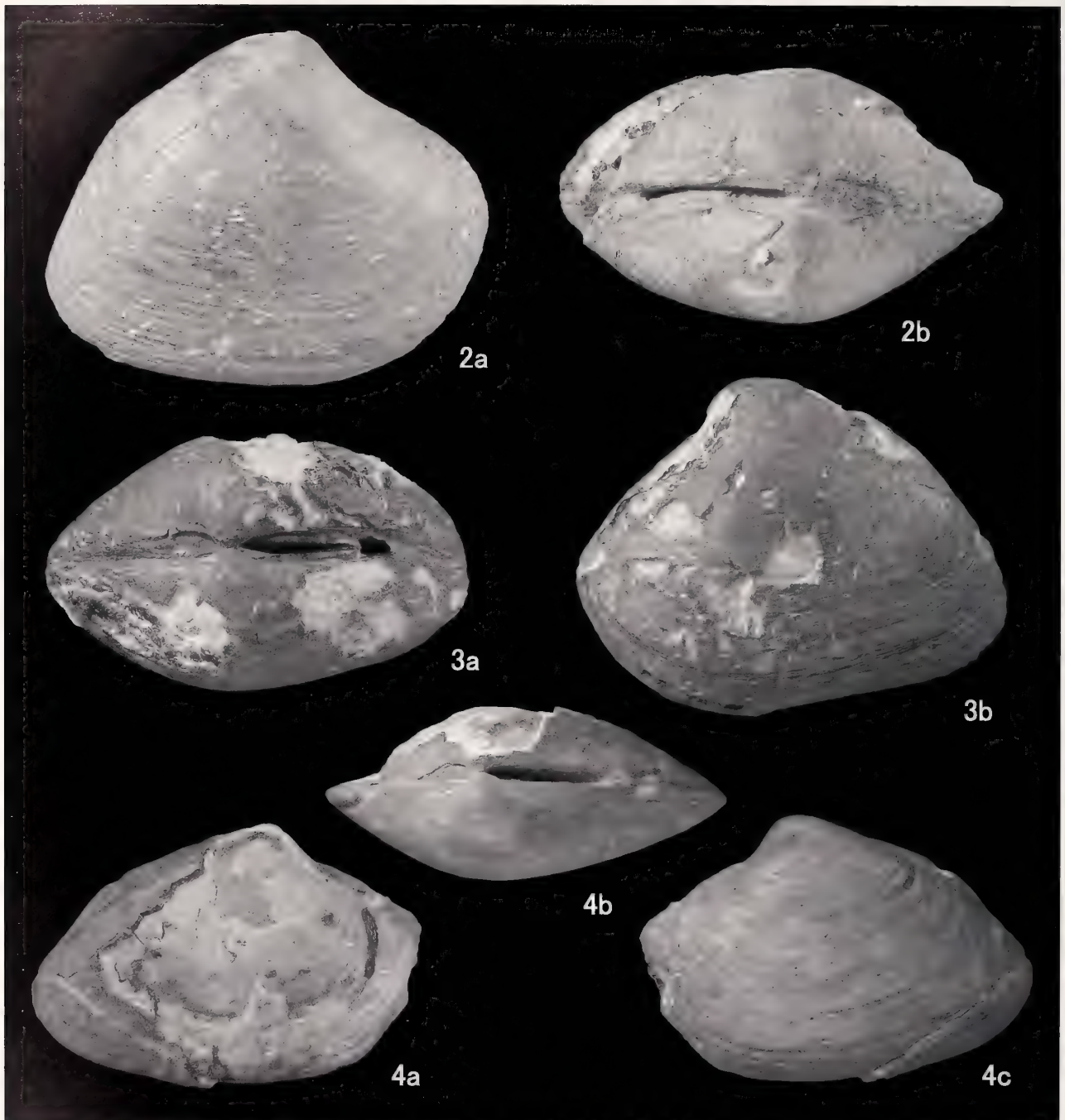
Type locality: Bed of Sanjussen-zawa Creek, 6.5 km upstream from where it flows into the Uryu River, Horokanai Town, Hokkaido (44°14'24"N, 142°5'26"E); My 4 Member of the Tenkaritoge Formation (locality R7203 by Nishida et al., 1998).

Stratigraphic and geographic distribution: Late Cretaceous (early Cenomanian); known only from the type locality.

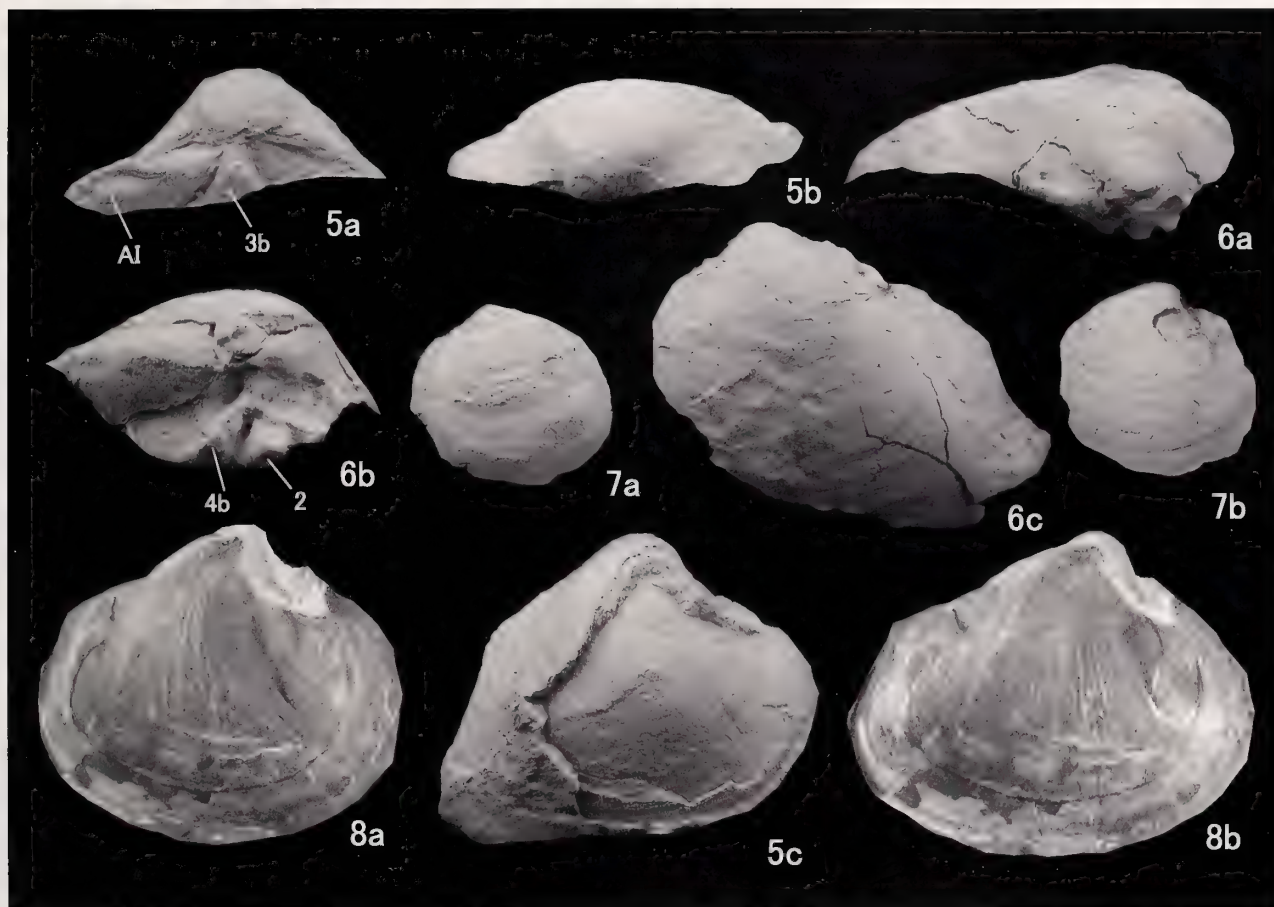
Original description: “Large shell (length [L] L = 130 mm in holotype and probably gerontic stage) probably of rounded triangular form (height [H] H/L = 0.8). Umbo (shell apex) situated almost centrally, 45–46% from anterior margin. Strongly inflated valve ([H]/breadth [B], H/B ≠ 0.68). Shells of right and left are equivalved. Posterior end is truncated. In the juvenile to middle growth stage represented by paratype (L = 88.6 mm), the shell height is shortened (H/L = 0.68). Postero-dorsal end is truncated meeting with the posterior margin. Lunule and hinge form is the same as gerontic one. There is a lunule at antero-dorsal part. The ventral margin is weakly arched. Ligament probably external and long on the basis of morphology of the hinge area at postero-dorsal part. Test is very thick about 7 mm at the ventral margin. Shell surface is ornamented by concentric growth lines. The umbo bends strongly inside, where characteristic subumbonal pit exists at the inside of the shell apex.”

Supplementary description: Shell large in size (up to 157.5 mm in length), thick, well inflated in adult specimens, veneriform, rather equivalve, slightly inequilateral. Small specimens less inflated and *Felaniella*-like in shape. Umbo projecting above dorsal margin, prosogyrate, situated anteriorly at two-fifths of shell length. Anterodorsal margin broadly arcuate, grading into rounded anterior margin; ventral margin broadly arcuate; posterodorsal margin straight, gradually sloping, forming blunt angle with subtruncated posterior margin. Surface smooth except for rough and low commarginal lamellae; coarse concentric ribs visible in right valve of a small specimen. Shallow radial sulcus running from beak to posterior end in large specimens.

Hinge plate wide; right valve with one stout and triangular central tooth (3b), one elongate anterior



Figures 2–4. Type material of *Ezolucina inflata* (Kanie & Nishida). Figure 2. Holotype, length = 131.8 mm, YCM-GP1173. Figure 2a. Lateral view of right valve. Figure 2b. Dorsal view showing a posterior radial sulcus and deeply impressed lunule. Figure 3. Topotype, length = 157.5 mm+, YCM-GP1177. Figure 3a. Dorsal view. Figure 3b. Lateral view of left valve. Figure 4. Paratype, length = 82.6 mm, YCM-GP1174. Figure 4a. Lateral view of right valve. Figure 4b. Dorsal view showing a posterior radial sulcus and deeply impressed lunule. Figure 4c. Lateral view of left valve.



Figures 5–8. Additional specimens of *Ezolucina inflata* (Kanie & Nishida). Figure 5. Topotype, length = 28.9 mm, JUE no. 15854. Figure 5a. Hinge of right valve showing one strong cardinal and distinct anterior lateral tooth, length of hinge plate = 21.3 mm. Figure 5b. Dorsal view showing deeply depressed lunule. Figure 5c. Lateral view of right valve. Figure 6. Topotype, length = 39.9 mm+, JUE no. 15856. Figure 6a. Dorsal view of left valve showing deeply impressed lunule. 6b. Hinge of left valve showing two strong cardinal teeth, length of hinge illustrated here = 21.8 mm. 6c. Lateral view of left valve. Figure 7. Topotype, length = 15.4 mm, JUE no. 15855. Figure 7a. Lateral view of left valve. Figure 7b. Lateral view of right valve having rude concentric ridges. Figure 8. Topotype, length = 33.7 mm, JUE no. 15853. Figure 8a. Lateral view of right valve stressing anterior adductor scar. Figure 8b. Normal lateral view of right valve.

lateral tooth (AI) parallel to hinge base, and a weak blunt node just below deeply impressed lunule; left valve with strong anterior cardinal (2), touching deeply impressed lunule, posterior tooth (4b) rather thin. Ligament occupying two-thirds of posterodorsal margin. Anterior adductor scar elongate quadrate, moderate in size (adductor length = 9.1 mm in JUE no. 15853; adductor length/shell length = 0.27) and about 75% of its length detached from pallial line (maximum distance from pallial line = 1.9 mm in JUE no. 15853); posterior adductor scar pear-shaped. Inner surface covered by coarse and distinct radial striations (Figure 9). Lunule broadly lanceolate, well defined, deeply impressed, slightly asymmetrical, slightly larger in right valve than in left valve, and occupying one-third of anterodorsal margin. Pallial line narrow, well-

developed, entire, and quite distant from shell margin. Inner ventral margin smooth.

Remarks: Very similar to *Ezolucina inflata* in shell shape and size is '*Lucina*' *colusaensis* Stanton, 1895, a species that is apparently restricted to Upper Jurassic (Tithonian) to Lower Cretaceous (Hauterivian) cold-seep carbonates in northern California, USA (Stanton, 1895, p. 60, pl. 11, figs. 4, 5; Campbell, 2006; Kiel et al., 2008). Compared to our material of *Ezolucina inflata* the thickness of '*Lucina*' *colusaensis* resembles that of the less inflated specimens of *Ezolucina inflata*. Unfortunately, '*Lucina*' *colusaensis* is usually poorly preserved and features of the interior of this shell are unknown (Stanton, 1895; SK, pers. observation; K.A. Campbell, personal communication 2007); thus a

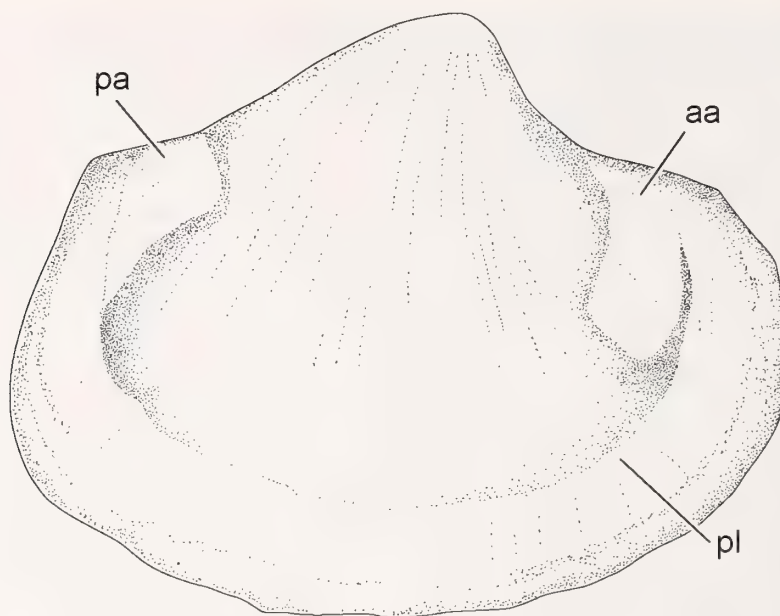


Figure 9. Muscle scars and pallial line of *Ezolucina inflata* (Kanie & Nishida) based on JUE no. 15853. Abbreviations: aa, anterior adductor scar; pa, posterior adductor scar; pl, pallial line.

confirmation of its generic position must await the availability of well-preserved specimens.

Another large lucinid with prominent umbos is *Saxolucina* (*Megaxinus*) *matsushitai* Matsumoto (1971, p. 663–665, pl. 1, fig. 1, pl. 2, figs. 1–3) from the Oligocene Setogawa Group [now considered as Miocene in age; see Watanabe (1988)] in central Japan, but this species is clearly distinct from *Ezolucina inflata* by having a less inflated shell with an edentulous dentition.

Ezolucina inflata resembles *Here excavata* (Carpenter, 1857) in having a deeply depressed lunule, one cardinal tooth and anterior lateral tooth in the right valve, and two cardinal teeth in the left valve. However, *Here excavata* differs from *Ezolucina inflata* by its subcircular shell with concentric lamellae, many fine ventral crenulations and more deeply sunken lunule. Its veneriform shape with the strongly sloping posterodorsal margin sets *Ezolucina inflata* apart from most other Cretaceous lucinids, which mostly have a nearly round outline (e.g., *Discoloripes septentrionalis* Kelly, 1992; “*Lucina*” spp. in Stephenson, 1952; *Callucina olea* Vokes, 1946; “*Lucina*” *aquensis* Holzapfel, 1889, p. 188, pl. 19, fig. 4). A lucinid with similar hinge dentition was described and figured as *Lucina subnummismalis* d’Orbigny, 1850 from the Campanian Vaals Greensand of Germany (Holzapfel, 1889, p. 187–8, pl. 19, figs. 1–3). This species is distinct from *Ezolucina inflata* because it is very flat, has distinct commarginal ribs, and lacks the strongly sloping posterodorsal margin of *Ezolucina inflata*. Also “*Lucina* aff. *valentula* de Lor.” described by Ascher (1906,

p. 161, pl. 14: 5) from a potential Hauterivian seep site in eastern Czech Republic lacks the strongly sloping posterodorsal margin of *Ezolucina inflata*.

DISCUSSION

Examination of the type and additional specimens clearly shows that *Vesicomya inflata* is a member of Lucinidae because it has the hinge structure and the adductor muscle scar and pallial line patterns typical of Lucinidae (i.e., a lucinoid hinge dentition, a broadly lanceolate, asymmetric, sunken lunule, and an elongate anterior adductor muscle scar detached from the pallial line). The previous assignment of this species to the Vesicomidae was due to the superficial resemblance in shell outline and the lack of the information on the shell interior. The new monotypic genus *Ezolucina* based on *V. inflata* is more elongate than most lucinids and has moderately prominent umbones somewhat suggestive of a vesicomid or an eomiodontid. However, shells of these families can easily be distinguished from those of the Lucinidae by their hinge and muscle scar patterns.

In their compilation of the stratigraphic ranges of mollusks at cold seeps, Kiel & Little (2006) listed *V. inflata* as the oldest fossil occurrence of *Vesicomya*, based on the available literature (Kanie & Nishida, 2000). When Amano & Kiel (2007) subsequently revised the North Pacific fossil record of the Vesicomidae, they could not confirm any of the previous records of this genus. One of the oldest “small” vesicomids related to *Vesicomya* (cf. Cosel & Salas,

Table 2

Faunal list based on fossils that we collected from the type locality of *Ezolucina inflata* (Kanie & Nishida). All of these species possibly harbor symbiotic bacteria. Numbers indicate the number of recovered individuals, capital letters are sample designations.

Species	Carbonate no. (HRK -)	A	B	C	D
<i>Acharax cretacea</i> Kanie and Nishida					2
<i>Nucinella</i> ? sp.					1
<i>Ezolucina inflata</i> (Kanie and Nishida)	3			2	4
<i>Miltha</i> ? sp.			1		
<i>Thyasira</i> ? sp.					1

2001; Krylova & Sahling, 2006) is “*Vesicomya kawadai* (Aoki, 1954) from the lower Miocene Taira Formation in Fukushima Prefecture, Japan (Aoki, 1954; Kamada, 1962), but more material is required to confirm its generic position. Another certain record of a “small” vesicomylid is *Isorropodon frankfortensis* Amano & Kiel, 2007 from the lower Miocene Astoria Formation in Washington State, USA.

Kanie et al. (2000) suggested that the carbonate concretions from Sanjussen-zawa Creek were ancient cold-seep deposits because of the presence of chemo-symbiotic species like solemyids, vesicomylids, and lucinids. Even when the vesicomylids are removed from this list, most taxa from these concretions (see Table 2) rely at least partly on symbiotic sulfur-oxidizing bacteria. However, the isotope data and the lithological observations presented here do not support a reconstruction as ancient cold-seep deposit. The data only suggests that these taxa lived in organic- and sulfide-rich sediment favorable for species with sulphophilic symbionts. Three of the five taxa from the concretions at Sanjussen-zawa Creek (*Acharax*, *Thyasira*, and *Miltha*) can also be found in the mudstone and siltstone of the Yezo Group (Tashiro, 2004) and their relative abundance at this site might be due their early diagenetic preservation in the concretions.

The exceptionally large size of *Ezolucina inflata* is remarkable; among Cretaceous lucinids it even exceeds that of the cold-seep restricted *Nipponothracia*. Among Recent species, it matches the size of *Meganodonta acetabulum* Bouchet & Cosel, 2004, recently described as the largest living lucinid from a depth of 256–472 m. The species was found in an area of presumed diffuse gas seepage and was associated with other bivalves bearing chemotrophic endosymbionts, like solemyids, thyasirids, and other lucinids. This set of taxa is similar to that associated with *Ezolucina inflata*, but our carbon isotope data do not indicate gas seepage in its environment. Most other modern deep-water lucinids rarely exceed 50 mm in length (Cosel, 2006) and are thus much smaller than *Ezolucina inflata*. However,

deep-water environments of the Late Cretaceous were inhabited by a number of exceptionally large taxa like bivalve *Inoceramus* or the capulid limpet *Gigantocapulus giganteus* (cf. Takahashi et al., 2007). Thus, the paleoenvironment of *Ezolucina inflata* remains enigmatic.

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A Quantitative Assessment of Spermatozoan Morphology in *Nutricola confusa* and *Nutricola tantilla* (Bivalvia: Veneridae)

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Abstract. The brooding bivalves, *Nutricola tantilla* and *N. confusa* overlap in their geographic distributions, habitats, and modes and timing of reproduction. Based on previous studies we infer that males of both species release spermatozoa into the water column; while females retain developing embryos in a brood chamber. Females release fully formed juveniles and there is no pelagic larval stage. We hypothesized that the muco-ciliary processes of particle selection and retention may act on differences in sperm morphology and contribute to reproductive isolation. We extracted sperm cells from both species and quantified nine linear measurements: the lengths of the acrosome, nuclear, midpiece and tail regions, and five different width measurements. We found significant differences in the lengths of the acrosome, midpiece, and tail. We also found that *N. confusa* produces dimorphic sperm and this is the first report of sperm dimorphism in the Veneroidea. Despite the significant differences in lengths, it is likely that other prezygotic mechanisms are responsible for reproductive isolation.

INTRODUCTION

Nutricola tantilla and *N. confusa* are morphologically similar, small bivalves (<10 mm shell length), that inhabit the top 2.5 cm of soft substrata in the intertidal to shallow-subtidal zones of protected bays of western North America (Coan et al., 2000). The reported geographic range of *Nutricola tantilla* is from Prince William Sound, Alaska to Isla Cedros, Baja California and *N. confusa* occurs from Coos Bay, Oregon to Carmel Bay, California. Where their ranges overlap they are sympatric and both species are very common in Bodega Bay, California (Grosholz & Ruiz, 1995). In earlier studies, the two species have been referred to as *Transeennella* and there is some disagreement over the taxonomy (Lindberg, 1990).

Females of both species are generally larger than males (Hansen, 1953; Asson-Bartres, 1988; Russell and Huelsenbeck, 1989). Hansen (1953) performed histological examinations of 371 specimens and found “5 were in a state of reversal from male to female” (p. 319). Some studies have cited this work as evidence for protandry (Kabat, 1985, 1986; Asson-Bartres, 1988) whereas Mottet (1988) attributes the size disparity to differential growth rates.

Both species lack pelagic larval stages and females brood their developing embryos and early juvenile stages in a pouch located between the inner demibranch and visceral mass (see figures 2 and 3 in Kabat, 1985 for detailed SEMs). Broods can be found throughout the year but there is seasonal variation in reproduction

with higher levels during the summer and fall (Asson-Bartres, 1988; Russell & Huelsenbeck, 1989). During peak periods of reproduction brood number can be as high as 300 and is a function of female size (Kabat, 1985; Russell & Huelsenbeck, 1989).

Sperm storage has not been reported in *Nutricola* (Mottet, 1988), we have not observed it, and therefore conclude that these species outcross. We infer that males release sperm into the water column because individuals produce only eggs or sperm at any one time and females retain their eggs for brooding. Sperm probably enter the mantle cavity of a female through the siphons. This fertilization mechanism, called “spermcast mating” (Bishop & Pemberton, 2006), has been proposed for other outcrossing brooding bivalves (Oldfield, 1964; Sellmer, 1967) and shown to be the method of sperm transfer for the brooding bivalve, *Mysella tumida* (O’Foighil, 1985b). Once inside the mantle cavity, the mechanics of directing sperm dorsally to the ovaries and unfertilized eggs is unknown but could involve chemotaxis and/or selective muco-ciliary activity of the gills.

Nutricola tantilla and *N. confusa* are sympatric, reproduce at the same time of year, and presumably females are exposed to sperm released from males of both species. One question that arises from these circumstances is how is reproductive isolation maintained? The purpose of our study was to quantify the gross morphology of spermatozoa from *N. tantilla* and *N. confusa* to determine whether differences in size/shape could contribute to the maintenance of reproductive isolation. This study represents the first attempt

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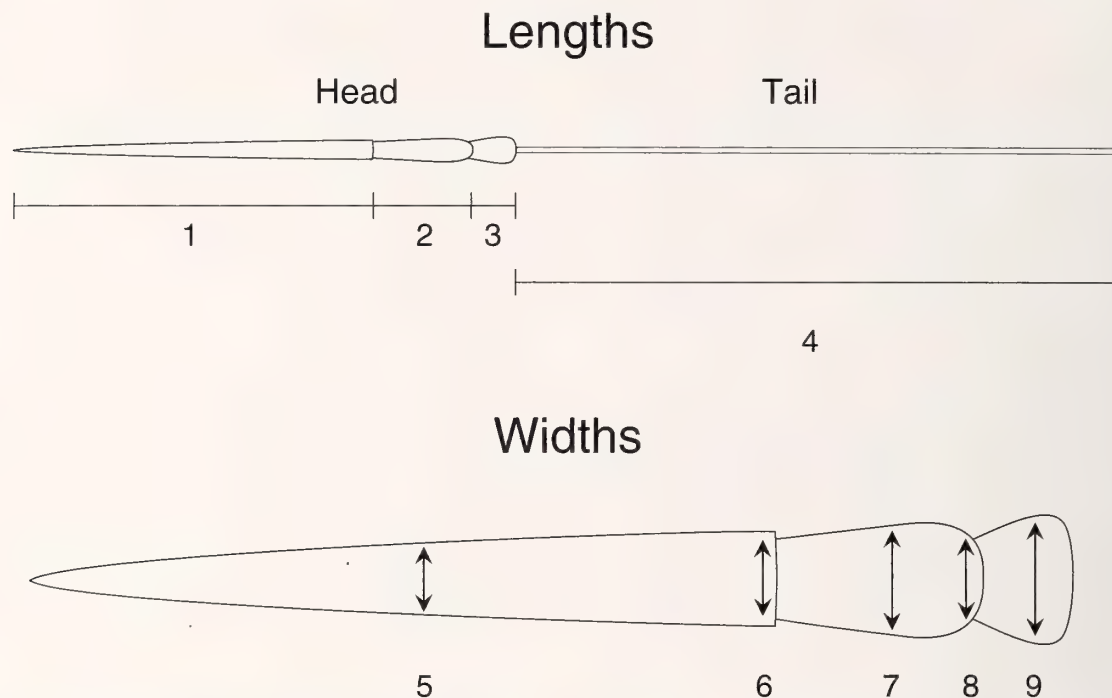


Figure 1. Schematic diagram of spermatozoa found in *Nutricula* illustrating the nine linear dimensions measured. Lengths: 1 = acrosome, 2 = nuclear region, 3 = midpiece, 4 = tail. Widths: 5 = acrosome midpoint, 6 = acrosome juncture with nuclear region, 7 = nuclear region midpoint, 8 = nuclear region juncture with midpiece, 9 = midpiece.

to quantify *Nutricula* spermatozoa morphology using electron microscopy.

METHODS AND MATERIALS

Samples of both species of clams were collected from Bodega Bay California on March 26, 2007, shipped overnight to Villanova University, separately maintained in a sea table (10°C and 32‰), and fed a mixture of phytoplankton cultures of *Tetraselmis* sp., *Thalassiosira* sp., *Isochrysis galbana*, and *Chaetoceros muelleri* until processed.

Attempts to induce spawning with thermal shocking methods (Castagna & Kraeuter, 1981; Deming & Russell, 1999) were unsuccessful so we resorted to extracting sperm via gonad squashes. Individuals of each species were dissected in separate containers of sea water. The gonads were removed, gently macerated, and released sperm in the sea water. Samples of the seawater were examined with a compound microscope for the presence/activity of spermatozoa. When active spermatozoa were identified, additional seawater samples with sperm were pipetted on to ploy-L-lysine coated cover slips. The sperm were fixed at 4°C in 2.5% glutaraldehyde in 0.1 M cacodylate buffer, adjusted to pH 7.4 and 900 mOsm with 0.4 M NaCl and 2 mM CaCl₂. After a rinse in the same buffer, samples were postfixed in 1% osmium tetroxide, in the same buffer,

and rinsed again. Samples were dehydrated in an ascending series of ethanol dilutions (25%, 50%, 75%, 95%, and 100%) and critical point dried using CO₂ as transitional fluid. Cover slips were sputter coated with gold/palladium and observed in a Hitachi S-570 SEM at 5 kV.

Digital images of intact spermatozoa were captured and then measured using ImageJ software version 1.37 V (Abramoff et al., 2004). Nine separate linear measurements were recorded on each intact spermatozoon (Figure 1): lengths of the acrosome, nuclear region, midpiece and tail; and widths of each of the three head regions (acrosome, nuclear, and midpiece) as well as the widths of the boundaries between adjacent head regions.

All data were tested for normality using a Shapiro-Wilk W test and the nine linear dimensions between species were compared using a t-test when both data sets were normally distributed, or a Wilcoxon Rank Sum test when either (or both) data sets were not normally distributed. A Principle Component Analysis (PCA) was used to combine all morphometric data to visualize the degree of separation between the two species based on spermatozoa morphology. Finally, a discriminant analysis was performed to assess how many of the samples would be correctly assigned to each species based on the nine linear measurements. All

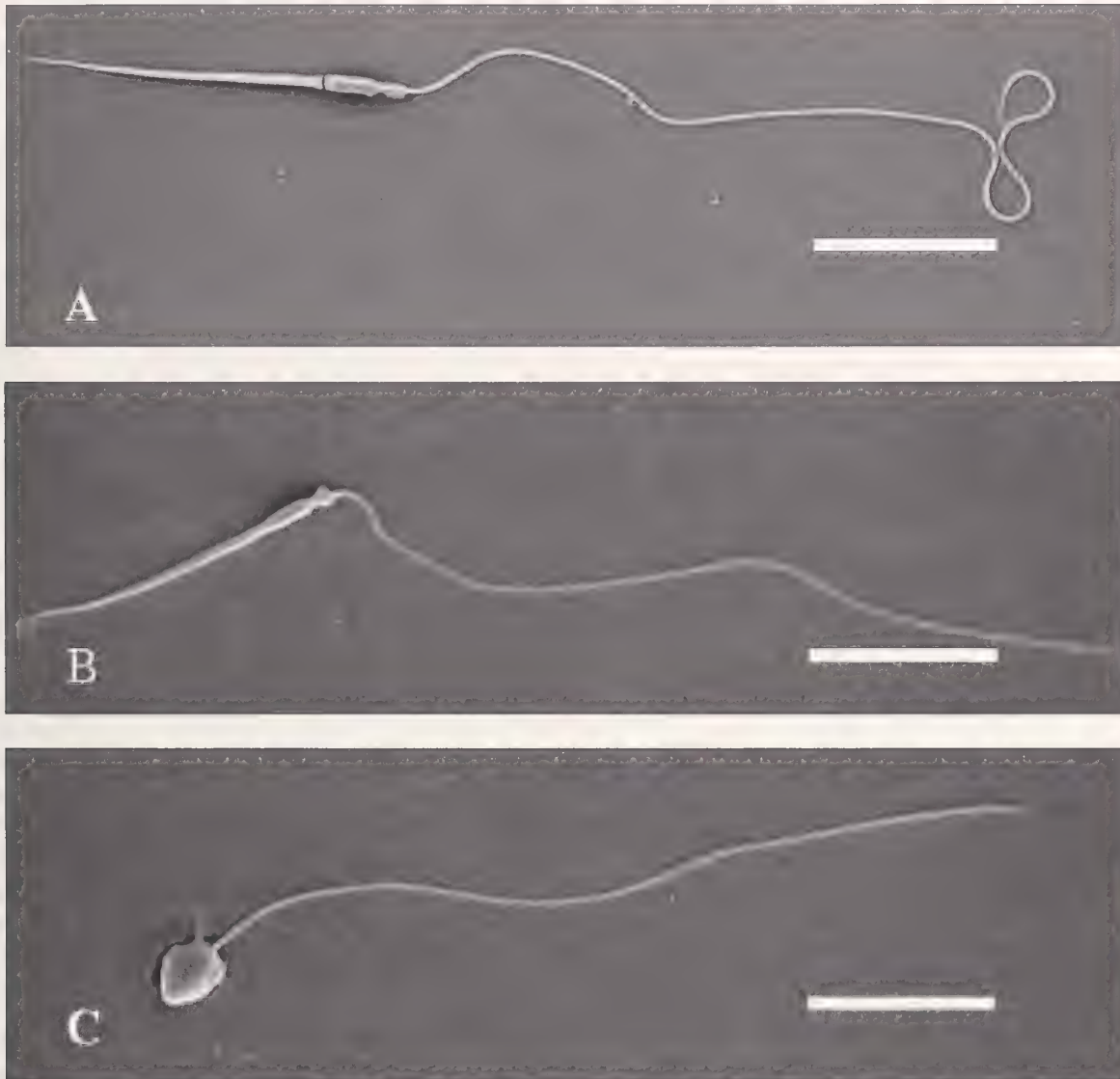


Figure 2. Examples of spermatozoa found in *Nutricola*. The scale bars = 10 μ m. A. *Nutricola tantilla*. B. *Nutricola confusa*. C. This type of sperm representing a distinct morphology (rounded-head) was found only in *N. confusa*.

analyses were performed using JMP (Version 4.04, SAS Institute Inc.).

RESULTS

Active sperm were found in all samples of male clams; 3 males were found for *N. tantilla* and 2 males for *N. confusa*. Electron microscopy preparations were processed for each male and intact spermatozoa were identified and measured for both *N. tantilla* ($n = 13$) and *N. confusa* ($n = 18$). Both species exhibited markedly elongated heads and examples of these cells illustrating the three distinct regions of the head are shown in Figure 2. Furthermore, a morphologically

different sperm with a round head was found only in samples from *N. confusa* (Figure 2C).

Significant differences in the lengths between the species were found in the acrosome ($Z = 2.62$, $P = .0087$), tail ($Z = 3.70$, $P = .0002$), and midpiece ($t = 4.39$, $P = .0001$) regions. In all three cases the spermatozoa of *N. tantilla* were significantly longer than *N. confusa* (Figure 3). No significant difference was found in any of the width measurements or the length of the nuclear region. The range-frame box and whiskers plots show that although the spermatozoa from *N. tantilla* are longer, there is considerable overlap with *N. confusa* (Figure 3).

The results of a PCA are displayed in Figure 4 and a

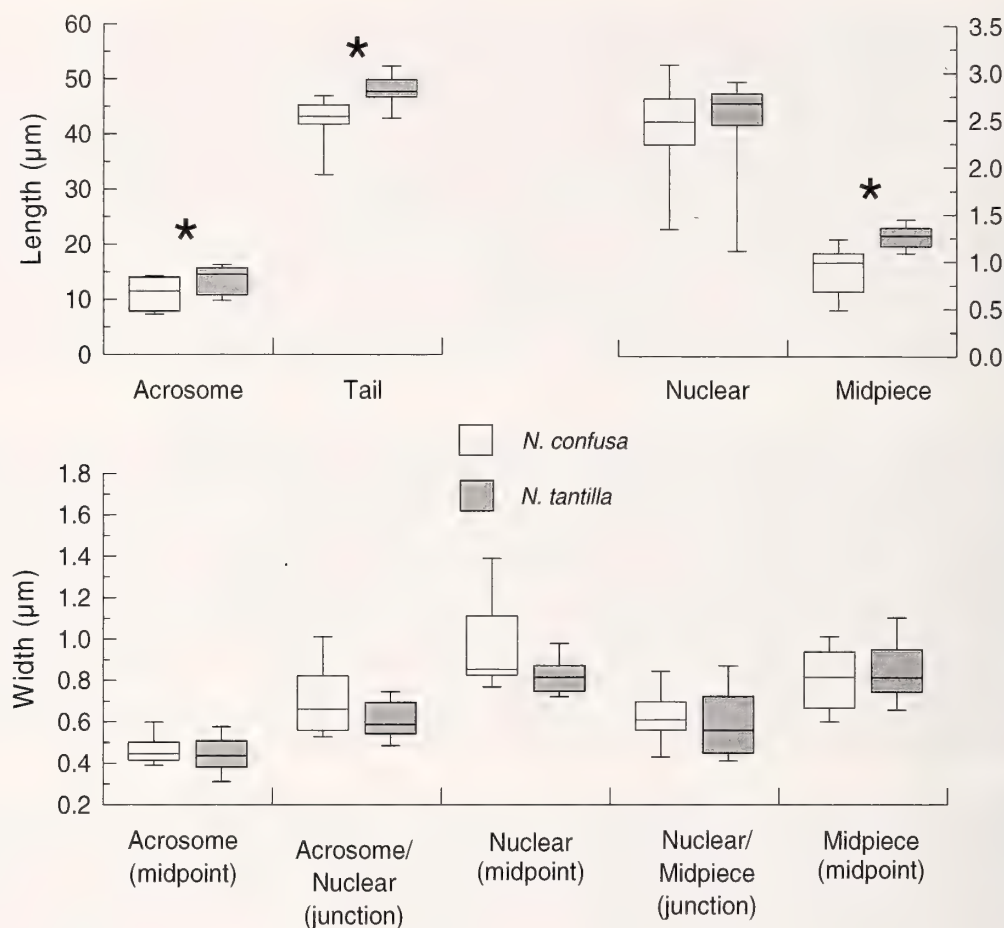


Figure 3. Box and whiskers plots of the nine linear measurements of *N. tantilla* (shaded) and *N. confusa* (open) spermatozoa. The horizontal lines within each box are the medians, the edges of the boxes are the 25th and 75th percentiles and the whiskers are the 5th and 95th percentiles. Significant differences (*) were found in the acrosome, tail, and midpiece lengths.

discriminant analysis correctly identified 87% (27 out of 31) of the measured spermatozoa.

DISCUSSION

Both species showed spermatozoa with elongated heads composed of three distinct regions (Figure 2). The designations of acrosome, nuclear, and midpiece (Figure 1) are based on the relative positions of these regions in the sperm of other taxa (Franzén, 1956) and comparison with the illustration and description of the spermatozoa of *Transennella* (= *Nutricula*) *tantilla* in (Thompson, 1973). The mean lengths of the acrosome, nuclear, and midpiece regions of *N. tantilla* from our samples are 13.68, 2.47, and 1.27 (μm) respectively, which are comparable to the lengths Thompson (1973) reported: 15.0, 2.4, and 1.0 (μm). Franzén (1983) noted that the acrosome is a "prominent structure" in bivalve spermatozoa (as is the case here) and commented on Thompson's (1973) description of *N. tantilla* sperma-

tozoa that "in spite of its unusual proportions [it] seems to belong to the primitive type."

Spermatozoa with a distinctly different morphology were found only in *N. confusa* (Figure 2C). We did not observe any intermediate stages between the "round headed" sperm and the mature sperm with the elongated acrosomes (Figure 2B). This observation strongly suggests the presence of sperm dimorphism in *N. confusa*. Sperm dimorphism is relatively uncommon in bivalves having been reported in only a few species (Ockelmann, 1965; Jespersen et al., 2001; Jespersen & Lützen, 2001; Lützen et al., 2001; Jespersen et al., 2002; Jespersen et al., 2004; Lützen et al., 2004). We found this second type of sperm in all of the SEM preparations of *N. confusa* and in none of the preparations from *N. tantilla*. This finding is the first reported case of sperm dimorphism in the Veneroidea. Other reports of sperm dimorphism occur in the Galeommatoidea where one species in one genus can exhibit sperm dimorphism, e.g., *Kurtiella bidentata* (as

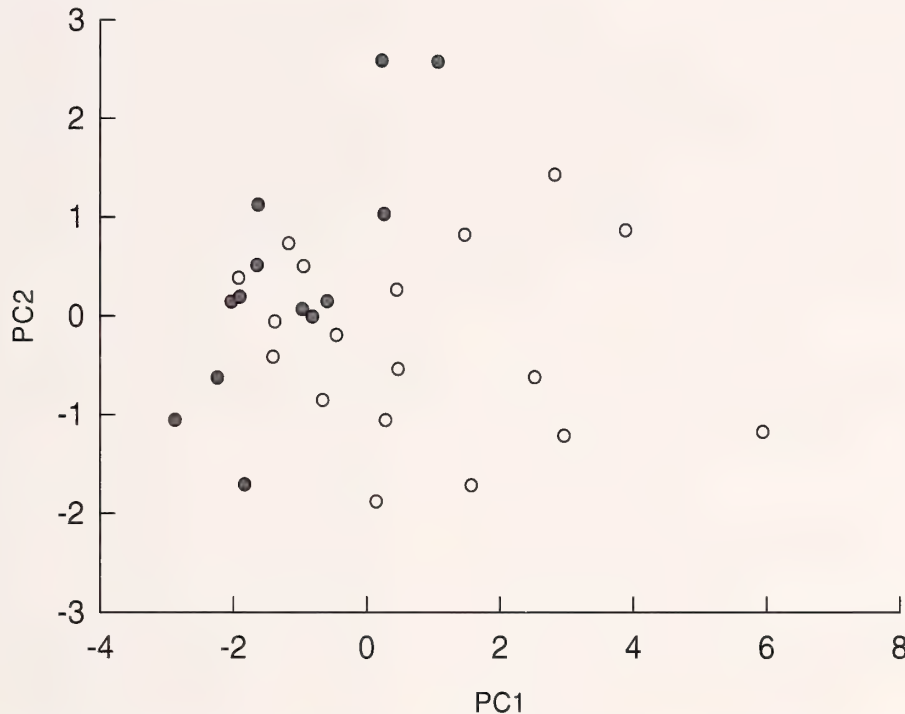


Figure 4. Results of Principle Component (PC) analysis using the nine measures illustrated in Figure 1. *Nutricula tantilla* (shaded, $n = 13$) and *N. confusa* (open; $n = 18$).

Mysella), and another closely related species does not, e.g., *M. tumida* (Ockelmann & Muus, 1978; O'Foighil, 1985a). It appears that this is the situation with the congeners *N. tantilla* and *N. confusa*.

The acrosome, midpiece and tail of the *Nutricula tantilla* sperm are significantly longer than those of *N. confusa* but no differences were found in the length of the nuclear region or any of the five width measurements (Figure 3). There is a significant difference in the overall mean lengths of spermatozoa – *N. tantilla* $65.26 \mu\text{m} \pm 4.64$ and *N. confusa* $56.93 \mu\text{m} \pm 5.73$ (\pm SD, $Z = 3.78$, $P = .0002$). Although there are significant morphological differences between the sperm in these species there is also considerable overlap in the variables measured. This point is illustrated by the PCA plot (Figure 4) which shows a limited degree of separation between the two species.

There are at least three hypotheses for the functional significance of elongated sperm heads in bivalves. Recently, Jespersen & Lützen (2007) proposed that this morphology allows sperm cells to better circumvent retention by the gills thus facilitating fertilization. Franzén (1983) found that elongated sperm heads are correlated with larger eggs and may aid in sperm penetration. Finally, Jespersen et al. (2001) proposed that the elongated sperm heads of the euspermatozoa of *Pseudopythina macrophthalmensis* may promote storage of sperm in seminal receptacles. Neither *N.*

tantilla nor *N. confusa* have seminal receptacles and do not store sperm so the later hypothesis does not apply to these species. However, the unusually long sperm heads of *N. tantilla* and *N. confusa* could function in either gill circumvention or penetration of the large lecithotrophic eggs.

The study of the muco-ciliary processes of particle selection and retention in bivalves has a long and rich history (see Ward & Shumway, 2004 for review). The focus of these studies has been on feeding biomechanics and the ecological role bivalves play in benthic-pelagic coupling processes. During preingestive processing, “there are opportunities for particle selection based upon quantitative and qualitative aspects of the particles” (Ward & Shumway, 2004:85). Spermatozoa cells of spermcast-mating, brooding bivalves like *Nutricula*, are within the size-range of particles selected via the muco-ciliary processes (Møhlenberg & Riisgård, 1978) and are likely subject to these processes. The differences in sperm morphology demonstrated here while significant, are probably insufficient by themselves to account for species-specific spermatozoa recognition. These species produce hundreds of eggs compared to the hundreds of thousands produced by broadcast spawning taxa and cannot afford postzygotic isolation. Therefore it is likely that factors other than spermatozoa morphology play a role in maintaining reproductive isolation via prezygotic mechanisms.

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Effects of Estivation on the Concentrations of Selected Carboxylic Acids of Two Strains of *Helisoma trivolvis*

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Abstract. High-performance ion exclusion column liquid chromatography was used to analyze the effects of estivation on certain carboxylic acids in the digestive gland-gonad complex (DGG) of a Pennsylvania (Pa) and Colorado (Co) strain of *Helisoma trivolvis*. The DGG samples were extracted using 50% Locke's solution, followed by cleanup using anion-exchange solid phase extraction and analysis by ion exclusion high performance liquid chromatography with ultraviolet detection. Succinic, pyruvic, malic, and fumaric acids were detected and quantified in the DGGs of both estivated and unestivated snails at concentrations ranging from 0.91 to 2200 ppm. There was a significant (Student's *t*-test, $P \leq 0.05$) reduction in the concentrations of succinic, pyruvic, and malic but not of fumaric acid in unestivated versus estivated *Helisoma trivolvis* (Pa). For *Helisoma trivolvis* (Co), there was a significant increase in succinic but not in fumaric, pyruvic, or malic acids in unestivated versus estivated snails. The reduction of certain carboxylic acids in the DGG of *Helisoma trivolvis* (Pa) suggests that estivation stimulates a decreased production of these acids or increased utilization by the snail tissue. Differences in the concentrations of certain acids between *H. trivolvis* (Pa) and *H. trivolvis* (Co) probably reflect strain differences.

INTRODUCTION

Estivation (also written as aestivation) of pulmonate snails in the family Planorbidae relates to a dormancy of these snails under conditions of drying out. Estivation allows the snails to survive long periods of drought. Moreover, snails infected with larval trematodes may retain their infections during estivation and transfer of the larval parasites to new hosts may occur when the snails emerge from estivation following submersion in fresh water. In the field, such estivation occurs when snails are subjected to drying conditions in lakes or ponds during short term or extended periods of drought. In the laboratory, estivation can be induced by subjecting the planorbids to a high relative humidity (circa 98%) and temperatures of about 22 to 24°C in a moist closed chamber as described by White et al. (2007). During estivation, snail metabolism is reduced and the organisms do not feed on exogenous food stuff. Information at the cellular and molecular level of the effects of estivation on planorbids is sparse. In our laboratory, we have begun estivation studies on planorbids in the genera *Biomphalaria* and *Helisoma*. Snails in these genera are important vectors of larval trematodes and nematodes and are associated with the transmission of numerous helminthic diseases to humans and wildlife; planorbid snails in these genera also serve as models for various research studies in the

biomedical sciences. Our studies to date on the topic have examined the effects of experimentally-induced estivation on various analytes in both uninfected and infected planorbids in the genera *Biomphalaria* and *Helisoma*. In general, our snail estivation studies have demonstrated a reduction of most of the analytes we examined and in most cases parasitism by larval trematodes has exacerbated the effects of estivation on diminution of certain metabolites in the snails. The studies reported in this paper are a continuation of the effects of estivation on analytes in two strains of planorbid snails in the genus *Helisoma*. More information on the rationale for the present work is given in the paragraphs below.

We maintain two strains of *Helisoma trivolvis* (Say, 1816) in our laboratory, one of which is *H. trivolvis* (Co) and the other *H. trivolvis* (Pa). The Co strain lacks melanin, is refractory to infection with miracidia of all trematodes tested to date, and is easy to culture in the laboratory (Schneck & Fried, 2005). It is also used as a model in invertebrate neurobiology (Kater, 1974). The Pa strain is ubiquitous in lakes and ponds in North America, is pigmented with melanin, and is infected with various species of larval trematodes (Schmidt & Fried, 1997).

Recent studies in our laboratory have examined the effects of estivation on various analytes in *Biomphalaria glabrata* (Say, 1816). Studies on lipids (White et al., 2006), carbohydrates (Jarusiewicz et al., 2006) and lipophilic pigments (Arthur et al., 2006) in the DGGs

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of these snails showed a decrease in these analytes as a function of snail estivation. One study on carboxylic acids in *B. glabrata* has determined changes in certain acids as a function of infection with *Schistosoma mansoni* larvae (Massa et al., 2007). One study on *B. glabrata* showed alterations in the concentrations of certain carboxylic acids as a function of estivation (Bezerra et al., 1999). Detailed studies on effects of estivation on the carboxylic acid content of any strain of *H. trivolvis* are not available. Therefore, the purpose of this study was to determine the effects of estivation on certain carboxylic acids in both the Pa and Co strains of *H. trivolvis*.

MATERIALS AND METHODS

Snail Maintenance

H. trivolvis (Co) has been maintained in our laboratory in continuous culture since the mid 1980s. This strain is maintained in Mason jar cultures, 15 to 20 snails per jar, in 800 mL of aerated artificial spring water (ASW). For further details, including the formulation of the ASW, see Schneck & Fried (2005). *H. trivolvis* (Pa) is available from April through November from local farm ponds and lakes in Northampton County, Pa (see Schmidt & Fried, 1997 for details). *H. trivolvis* (Pa) can be collected in the wild, brought into the laboratory, and maintained there for several months using the same cultivation procedure described for *H. trivolvis* (Co). Because some of these snails may be naturally infected with larval trematodes, they were examined by routine snail isolation procedures for larval trematodes; infected snails were removed from cultures and discarded.

Estivation

Usually 5 to 15 *H. trivolvis* (Pa) snails of each strain were estivated for 2, 3, or 7 days and a similar number of *H. trivolvis* (Co) for 7 days in a moist chamber at 24°C and a relative humidity of 98%. Details of the estivation chamber design were given in White et al. (2006). Preliminary studies showed that *H. trivolvis* (PA) did not survive the effects of estivation as well as *H. trivolvis* (Co), and therefore we used shorter estivation times for the studies on *H. trivolvis* (Pa).

At the end of each estivation period, snails were tested for survival by immersing them in ASW. Live snails became activated within 0.5 hr in ASW as shown by the extension of the head foot through the aperture. Snails that did not extend the head foot through the aperture were examined by mechanical probing with a needle after the shells were removed. Those that were not responsive were considered dead. The number of snails that survived estivation was recorded. Controls (unestivated snails) were maintained in Mason jar

cultures and fed leaf lettuce as described above for the same times as those that estivated.

Sample Preparation

Each snail was removed from the ASW and placed in a Petri dish. The shell was cracked gently and removed from the snail body. The DGG was dissected from the body and homogenized with 6 mL of 50% Locke's solution with a glass homogenizer. The homogenizer was washed with 2–3 mL of solution, which was then added to the homogenate. The DGG homogenate was centrifuged at 2500 g for 10 min at 25°C. The carboxylic acids were recovered from the supernatant by solid-phase extraction (SPE) as described below. Each sample represented the supernatant of one DGG and had a final volume of 8 ± 1 mL.

Carboxylic Acid Extraction

SPE was performed as outlined by Massa et al. (2007a). The acids were extracted from the DGG homogenate using Varian strong anion exchange columns (quaternary amine; 100 mg; 3 mL, Varian Inc., Palo Alto, Ca, USA). Under vacuum, the columns were cleaned and activated with 1 mL of 0.5 M HCL, 1 mL of methanol, and 2 mL of deionized (DI) water. The DGG homogenate supernatant was then passed through a column under vacuum. The column was cleaned again with 2 mL of DI water. The carboxylic acids were eluted from the columns using 1 mL of 0.5 M sulfuric acid.

HPLC Analysis

Acetic, fumaric, lactic, malic, pyruvic, and succinic acid salts were purchased from Sigma (St. Louis, Mo, USA). Stock solutions of each organic acid were prepared at a concentration of 1.00×10^3 ppm in 0.5 M H₂SO₄ and the stock solutions were diluted to 10, 25, 50, and 100 ppm.

High performance liquid chromatography (HPLC) was performed at 30°C using an Agilent Technologies (Wilmington, DE, USA) 1100 Series HPLC Instrument with an autosampler and ultraviolet (UV) detection at 210 nm. A Bio-Rad Laboratories (Hercules, CA, USA) Aminex ion exclusion HPX-87H column (300 × 7.8 mm) was used. 0.5 mM sulfuric acid was used as the mobile phase with an injection volume of 100 µL.

Linear calibration curves were generated using Microsoft Excel relating standard concentrations to their peak areas. The interpolated amounts of each organic acid quantified by HPLC were calculated using the following equation:

Table 1

Carboxylic acid concentrations in the digestive gland-gonad complex (DGG) of unestivated and estivated *H. trivolvis* (Pa).

Acid	Unestivated DGG		Estivated DGG (2 Days)	
	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)
Fumaric	18	100 ± 8.0	11	96 ± 8.5
Malic	9	450 ± 85	5	290 ± 53
Pyruvic	8	20 ± 5.7	4	19 ± 2.9
Succinic	10	350 ± 66	6	540 ± 180

Acid	Unestivated DGG		Estivated DGG (3 Days)	
	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)
Fumaric	16	130 ± 18	7	140 ± 13
Malic	9	270 ± 35	7	$<2.0^*$
Pyruvic	10	23 ± 7.4	7	$<2.0^*$
Succinic	9	280 ± 36	7	$<2.0^*$

Acid	Unestivated DGG		Estivated DGG (7 Days)	
	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)	Sample Size	ppm ($\mu\text{g/g} \pm$ Standard Error)
Fumaric	8	120 ± 8.8	4	98 ± 16
Malic	7	350 ± 54	4	$<2.0^*$
Pyruvic	6	34 ± 10	4	$<2.0^*$
Succinic	6	550 ± 150	4	$<2.0^*$

* A significant reduction in the concentration of carboxylic acids in the estivated DGG relative to the controls (Student's *t*-test, $P \leq 0.05$).

$$\text{Organic Acid (ppm)} = \frac{(I)(V)}{(M)}$$

where I = instrument solution concentration (ppm) interpolated from the standard calibration curve, V = sample volume (mL), and M = snail DGG mass (g).

RESULTS

For *H. trivolvis* (Pa), a total of 22 of 60 snails survived estivation for 2, 3, or 7 days. Of these, 11 of 20 survived 2 days, 7 of 25 survived 3 days, and 4 of 15 survived 7 days. The organic acid content of these snails and of 42 unestivated snails was determined.

For *H. trivolvis* (Co), 7 of 12 estivated snails survived 7 days. As with the Pa strain, the organic acid content for the 7 estivated and the 8 unestivated Co strain samples was determined on the last day of estivation. *H. trivolvis* (Co) was more capable of surviving long-term estivation (7 days) than was *H. trivolvis* (Pa).

The DGG samples of both Pa and Co strains of *H. trivolvis* showed peaks with similar retention times to the standards. Typical retention times of the standards in minutes were as follows: pyruvic, 9.2; malic, 9.7; succinic, 12.2; lactic, 12.4; acetic, 14.9; and fumaric, 16.2.

The carboxylic acids and their concentrations in ppm detected in DGG samples of unestivated and estivated

snails of *H. trivolvis* (Pa) are listed in Table 1. Similar information on DGG samples of unestivated and estivated snails of *H. trivolvis* (Co) snails are listed in Table 2. Of all the acids tested (acetic, fumaric, lactic, malic, pyruvic, and succinic acids), all but acetic and lactic were consistently detected in DGG samples of unestivated snails of both strains.

For *H. trivolvis* (Pa) estivated for 2 days, fumaric, malic, pyruvic, and succinic acids were detected and quantified (Table 1). The Student's *t*-test ($P \leq 0.05$) showed no significant difference in the concentrations of these acids between the unestivated and estivated samples. For *H. trivolvis* (Pa) estivated for 3 and 7 days, concentrations of fumaric acid were at the levels of those in the unestivated cohorts, whereas the concentrations of malic, pyruvic, and succinic acids in these snails were below the detection of 2 ppm of the HPLC analysis determined by extrapolation from the standard calibration curves. At 3 and 7 days, the concentrations of malic, pyruvic, and succinic acids in the DGGs of estivated *H. trivolvis* were significantly lower than those in the unestivated cohorts.

For *H. trivolvis* (Co) maintained for 7 days, fumaric, malic, pyruvic, and succinic acids were detected in both estivated and unestivated snails (Table 2). There was no significant difference ($P \leq 0.05$) in the concentrations of fumaric, malic, and pyruvic acids in unestivated versus estivated snails (Table 2). There was a

Table 2

Carboxylic acid concentrations in the digestive gland-gonad complex (DGG) of unestivated and estivated *H. trivolvis* (Co).

Acid	Unestivated DGG		Estivated DGG (7 Days)	
	Sample Size	ppm ($\mu\text{g/g} \pm \text{Standard Error}$)	Sample Size	ppm ($\mu\text{g/g} \pm \text{Standard Error}$)
Fumaric	8	90 \pm 9.3	7	82 \pm 7.1
Malic	8	340 \pm 23	7	500 \pm 100
Pyruvic	8	16 \pm 1.8	7	30 \pm 6.5
Succinic	8	400 \pm 56	7	1300 \pm 280*

* A significant increase in the concentration of carboxylic acids in the estivated DGG relative to the controls (Student's *t*-test, $P \leq 0.05$).

significant increase ($P \leq 0.05$) in the concentration of succinic acid in estivated versus unestivated *H. trivolvis* snails at 7 days.

DISCUSSION

Bezerra et al. (1999) stated that estivation of *B. glabrata* resulted in decreased snail metabolic activity. They suggested that the process of snail estivation could be better understood by studying the effects of estivation on various snail analytes. Earlier studies have been done to determine how estivation affects certain metabolites in *Biomphalaria* snails. Perhaps the most noteworthy of these studies was that of Von Brand et al. (1957), who showed that lipids, polysaccharides, lactic acid and certain volatile organic acids were depleted in estivated *B. glabrata* compared with the non-estivated controls. Bezerra et al. (1999) noted various changes in the organic content of estivated versus non-estivated *B. glabrata*. White et al. (2006) found a significant decrease in depot fats (triacylglycerols) in estivated versus non-estivated *B. glabrata*. Jarusiewicz et al. (1996) found a decrease in maltose and glucose in estivated versus non-estivated *B. glabrata*. The above-mentioned studies all documented significant changes in certain key analytes associated with metabolism in estivated planorbids compared with the non-estivated cohorts. These changes reflect the decreased metabolic activity that occurs during the period of dormancy that we associate with estivation.

Certain carboxylic acids decrease with estivation in planorbid snails. Bezerra et al. (1999) showed that for *B. glabrata* estivated for 7 days, the concentration of pyruvic acid in the digestive gland decreased but that of lactic, succinic, malic, and acetic increased compared to the unestivated controls. They used the term digestive gland in their study, but presumably they were examining the DGG. The gonad is at the most distal part of the DGG and Bezerra et al. (1999) made no mention of removing the gonad from the digestive gland in their study. Our findings on *H. trivolvis* (Pa) estivated for 3 and 7 days also showed a decrease in

pyruvic acid in accord with the findings of Bezerra et al. (1999) on *B. glabrata*. In contrast to the findings of an increase in succinic and malic acids in estivated *B. glabrata*, we found a decrease in these two acids in *H. trivolvis* (Pa) estivated for 3 and 7 days. Our finding of an increase in succinic acid in the DGG of *H. trivolvis* (Co) estivated for 7 days is in accord with the increase noted by Bezerra et al. (1999) for *B. glabrata* for the same time. The significant changes in the concentrations of carboxylic acids in the DGGs of estivated planorbids is difficult to determine until more information is available on the metabolism of these snails during estivation.

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Cenozoic *Nacella* (Patellogastropoda: Nacellidae) from Peru and Chile: Filling in the Gaps

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Abstract. The limpet genus, *Nacella* Schumacher, 1817 (Patellogastropoda: Nacellidae), is noted for its adaptation to cold water at high austral latitudes. The finding of at least five new Pliocene species (*Nacella* (*Nacella*) *lacrima*, sp. nov.; *N. (Patinigera) oblea*, sp. nov.; *N. (Patinigera) chalaensis*, sp. nov.; *N. (Patinigera) intiforma*, sp. nov.; and *N. (Patinigera) oconaensis*, sp. nov.) and one new late Oligocene species (*N. (Patinigera) reicheae*, sp. nov.) from tropical latitudes of southern Peru, as well as the recognition of the southern Chilean *N. (Patinigera) nielsenii*, sp. nov., newly named and reassigned to the late early Miocene, demonstrates the ecological range of *Nacella* once overlapped that of its warm-water sister genus, *Cellana* H. Adams, 1869. While determining the time and place of *Nacella*'s origin awaits the discovery of additional fossils, those found so far show modern sub-Antarctic *Nacella* taxa may have had low-latitude ancestors.

INTRODUCTION

The patellogastropod genus, *Nacella* Schumacher, 1817, is comprised almost entirely of limpets living at high southern latitudes (Powell, 1973), including several taxa from southern Chile and Argentina (Valdovinos & R  th, 2005). Just one extant South American species, the Chilean *N. (Patinigera) clypeator* (Lesson, 1831), ranges into warmer waters of the southeastern Pacific Ocean (Ram  rez-B  hme, 1996; Valdovinos & R  th, 2005; V. Mogollon, written communication, 2008), as it did, too, during the Pleistocene (Herm, 1969). Other fossil Quaternary *Nacella* include the extant *N. (Patinigera) deaurata* (Gmelin, 1791) and *N. (Patinigera) magellanica* (Gmelin, 1791) from Patagonia, Argentina (Aguirre et al., 2005, 2006). Reported Pliocene examples of *Nacella* include *N. (Patinigera)* cf. *N. concinna* (Strebel, 1908) from lower upper Pliocene basaltic conglomerates on Cockburn Island, Antarctic Peninsula (Jonkers, 1988; Jonkers & Kelley, 1998) and *N. (Patinigera)* aff. *N. terroris* (Filhol, 1880) from coarse-grained sandstones of Chilo  , southern Chile (Watters & Fleming, 1972). A doubtful account exists of Miocene *N. deaurata* from Patagonia (Brunet, 1997), where mollusks from Quaternary marine terraces are interspersed among older Tertiary taxa of the Entremont Formation.

Molecular phylogenetic studies show extant *Nacella* to be a paraphyletic grade or monophyletic clade most closely related to a clade encompassing extant species of *Cellana* H. Adams, 1869 (Koufopanou, 1999; Harasewych & McArthur, 2000; Nakano & Ozawa,

2007; Yoon & Kim, 2007). *Cellana* presently ranges throughout the tropical Indo-Pacific region, with species also found in Japan, Australia, New Zealand and on the Juan Fernandez Islands, 700 kilometers west of Chile (Powell, 1973). Fossil *Cellana* have been reported from South Africa (Pliocene: Kensley, 1972), Australia and New Zealand (late Eocene, early Miocene, and Pliocene-Pleistocene: Powell, 1973; Beu & Maxwell, 1990), the Antarctic Peninsula (late Eocene: Stillwell & Zinsmeister, 1992), and Chile (Pliocene: Herm, 1969). An Early Cretaceous record from Australia, *Cellana carpentariana* Skwarko, 1966 (*cf.* Powell, 1973), remains unconfirmed. The oldest *Cellana* verified on the basis of shell microstructure is the late Eocene *C. ampla* Lindberg & Hickman, 1986, from Oregon. The timing and place of the *Nacella*-*Cellana* evolutionary split and the reasons for the Recent disjunct distribution of *Cellana* (mostly tropical, Indo-Pacific) and *Nacella* (mostly cold-water, Southern Ocean) are still disputed (Koufopanou et al., 1999; Goldstien et al., 2006; Nakano & Ozawa, 2007).

This paper fills biogeographical and temporal gaps in the history of *Nacella* with the description of five new Pliocene species from tropical latitudes of southern Peru: *N. (Nacella) lacrima*, sp. nov.; *N. (Patinigera) oblea*, sp. nov.; *N. (Patinigera) chalaensis*, sp. nov.; *N. (Patinigera) intiforma*, sp. nov.; and *N. (Patinigera) oconaensis*, sp. nov. The Pliocene nacellid from Chilo   is reassigned a late early Miocene age and formally named *N. (Patinigera) nielsenii*, sp. nov. *Nacella (Patinigera) reicheae*, sp. nov., from uppermost Oligocene beds of southern Peru, ranks as the oldest known *Nacella*. The newly established longevity of *Nacella*

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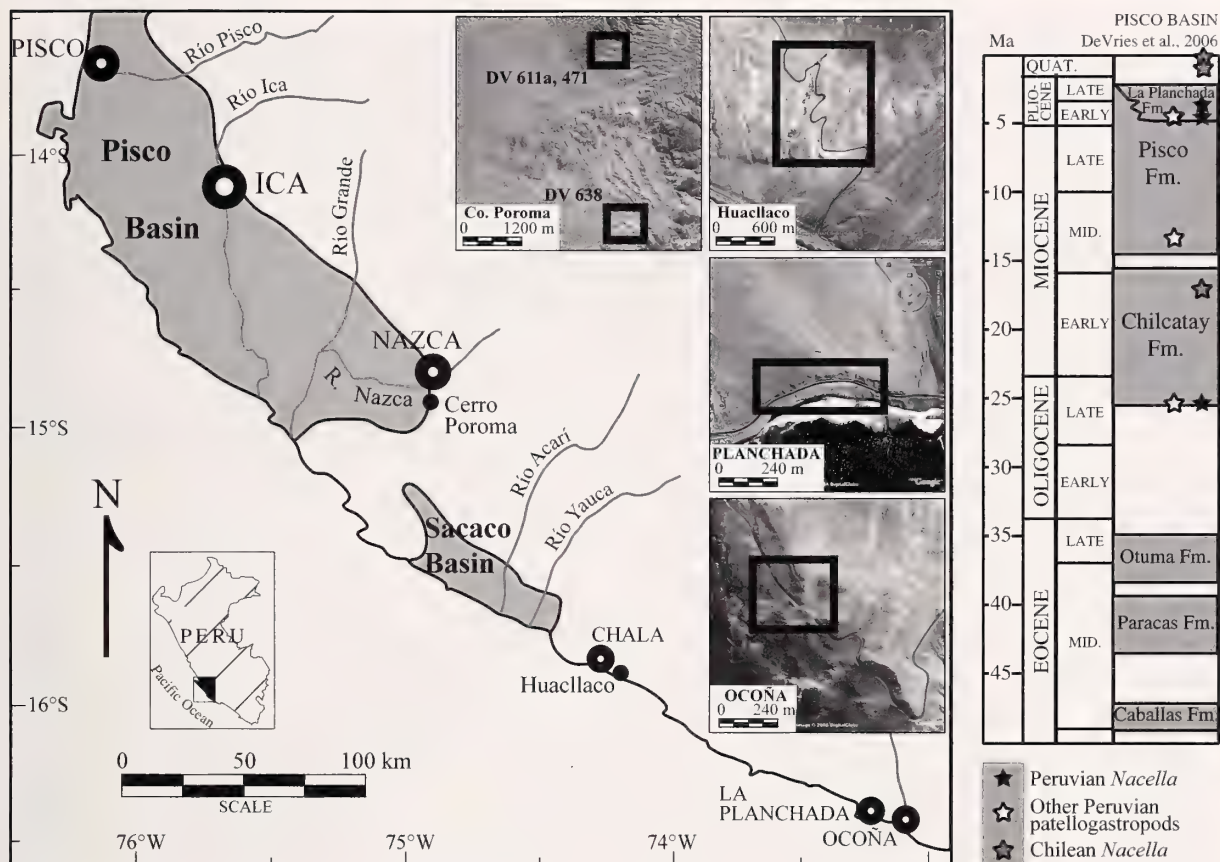


Figure 1. Location and Cenozoic stratigraphy of the Cenozoic Pisco and Sacaco forearc basins in southern Peru and type or other significant localities with *Nacella* specimens. Ocoña: type locality-sample (DV 1279-1) of *Nacella* (*Nacella*) *lacrima*, sp. nov., *N. (Patinigera) intiforma*, sp. nov., and *N. (Patinigera) ocoñaensis*, sp. nov. La Planchada: locality-sample DV 1267-1, with *N. intiforma*. Huacllaco: type locality-sample (DV 1254-2, DV 1254-bal6) of *N. (Patinigera) oblea*, sp. nov. and (DV 1628-1) *N. (Patinigera) chalaensis*, sp. nov. Cerro Poroma: type locality-sample (DV 611a-1) and locality-samples DV 471-1 and DV 638-1 with *N. (Patinigera) reicheae*, sp. nov. Road visible in each inset is the Pan-American Highway; images from Google Earth. Locality details are in the Appendix. Stratigraphic column shows temporal distribution of South American patellogastropods, including *Nacella* from Peru and Chile.

helps refine scenarios for its origin, while its low-latitude diversity challenges our understanding of the biogeographical constraints on its modern distribution.

GEOLOGY

The Cenozoic stratigraphy of southern Peruvian forearc basins was reviewed by DeVries (1998). *Nacella*-bearing beds were encountered at Cerro Poroma, near Nazca (Figures 1, 2F), where upper Oligocene bioclastic sandstone and conglomerate of the Chilcatay Formation onlap an Eocene peneplain, and farther south in the Pliocene La Planchada Formation, which is composed of balanid coquina, bioclastic conglomerate, coarse-grained bioclastic sandstone, and fine-bedded gravel (Beaudet et al., 1976), the remnants of littoral deposits dropped at the foot of steep sea cliffs.

Three outcrops of the La Planchada Formation along the Pan-American Highway deserve mention. A 70-meter measured section at Huacllaco (Figure 1) contains inferred upper lower Pliocene (Unit I) and upper Pliocene (Units II, III) bioclastic sediments capped by the most elevated and oldest marine terrace (Unit IV, uppermost Pliocene) (DeVries, 2003). Specimens of *Nacella* occur throughout the section, as do *Fissurella* and other littoral invertebrates that lived on rocky substrates (DeVries, 2003, 2006, 2007, 2008).

A second outcrop occurs in a quarry near Ocoña (Figure 1). The base consists of scour-bound lenses of angular boulders. Some lenses lack evidence of marine influence, but others have boulders encrusted with barnacles and oysters (Figure 2D). The rocky lenses are overlain with rippled and thin-bedded coarse-grained sandstone (Figures 2A, 2B) with scour-and-fill structures, imbricate slate pebbles, and ash laminae sur-

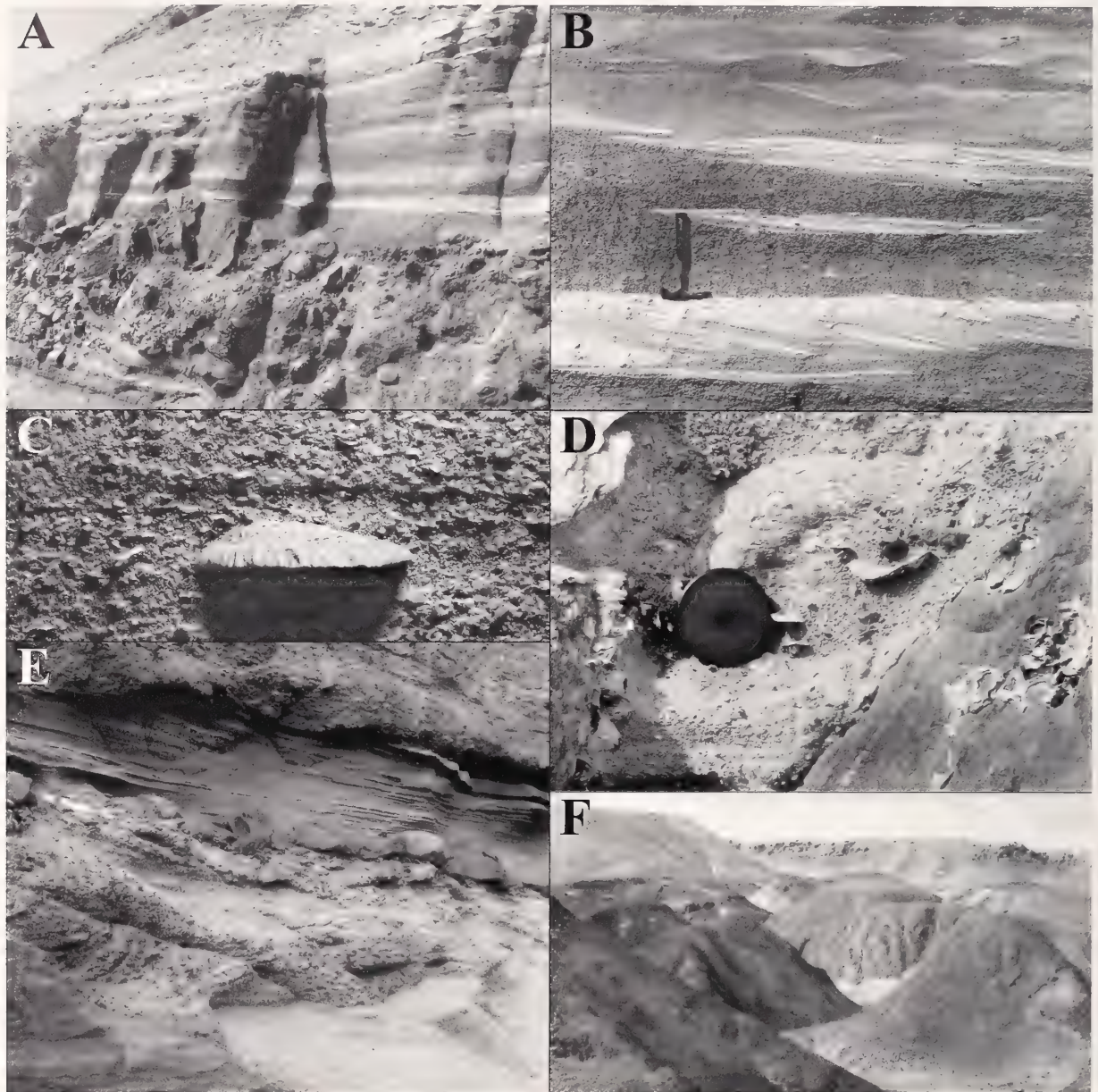


Figure 2. *Nacella* localities in southern Peru. A. Ocoña: interbedded rock-fall alluvium and finely bedded, tuffaceous, *Nacella*-bearing gravel and coarse-grained sandstone. B. Ocoña: cross-bedded and rippled tuffaceous gravel and sandstone containing *N. lacrima*, *N. intiforma*, and *N. oconaensis*. Shoreline is to left. C. Ocoña: close-up of *N. intiforma*, sp. nov., in fine-grained gravel. D. Ocoña: Debris-flow conglomerate with boulders encrusted with barnacles (left) and oysters (right). E. La Planchada: Finely bedded *Nacella*-bearing gravel, lowest left; early Pliocene cross-bedded bioclastic conglomerate, lowermost left-most set; Pleistocene cross-bedded bioclastic conglomerate, center; laminated sandstone and continental alluvium, upper left and right. F. Cerro Poroma: Post-Incaic granitic peneplain dissected by late Oligocene and modern erosional fissures, with continental volcanoclastics of early Miocene Nazca Group in background. Marine conglomerates with *Nacella reicheae*, sp. nov., occur in shallow fissures and at base of sedimentary sequence.

rounding small basement paleo-stacks, features that indicate a low-energy paleoenvironment in an otherwise high-energy setting, perhaps below wave base adjacent to steep sea cliffs (but see Cantalamessa & Di Celma (2005) for an interpretation of texturally

contrasting Chilean strata as paleotsunami deposits). Bedded marine deposits grade upwards into boulder-choked alluvium. The thin-bedded sandstone contains disarticulated flat-lying bioclasts of *Ostrea*, *Chlamys*, and *Nacella* (Figure 2C). A late early Pliocene age is

inferred from correlations with outcrops near Sacaco having age-diagnostic molluscan taxa (Muizon & DeVries, 1985; DeVries, 2003).

The third Pliocene *Nacella*-bearing outcrop is exposed south of La Planchada (Figures 1, 2E). The lithology and sedimentary textures are similar to those at Ocoña. The fauna consists of beds of disarticulated *Ostrea* valves, rare *Chlamys* valves, barnacles, and *Nacella*.

MATERIALS AND METHODS

Specimens of fossil Peruvian *Nacella* described in this study were found by the author unless noted otherwise. Examples of extant species of the patellogastropod genera *Lottia* Sowerby, 1834, *Cellana*, and *Scurria* Gray, 1847, were available for comparison. References to modern sea surface temperatures (SSTs) in western South America are based on the World Ocean Atlas 2005 (Locarnini et al., 2006).

Locality and sample descriptions are listed in the appendix. Lengths (L), widths (W), and heights (H) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Most figured specimens are coated with ammonium chloride. Types and other numbered specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM) and the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru (MUSM INV).

SYSTEMATIC PALEONTOLOGY

Order Patellogastropoda Lindberg, 1988

Family Nacellidae Thiele, 1891

Genus *Nacella* Schumacher, 1817

Type species: *Patella mytilina* Helbling, 1779. Recent, southern South America.

Discussion: The order Patellogastropoda encompasses taxa with conical shells having numerous anatomical synapomorphies (Lindberg, 1988; Sasaki, 1998); its monophyly is strongly supported by molecular data (Harasewych & McArthur, 2000; Nakano & Ozawa, 2007; Yoon & Kim, 2007). The phylogenetic relationships of families within Patellogastropoda, however, remain uncertain (Ridgway et al., 1998; Nakano & Ozawa, 2007). Some place Nacellidae or Nacelloidea (*Nacella* + *Cellana*) in a clade with Patellidae (Powell, 1973; Sasaki, 1998), others as a sister group to Acmaeoidea (Lindberg, 1988, 1998), still others as a monophyletic clade (Koufopanou et al., 1999), possibly related to Leptidae + Pectinodontidae (Nakano &

Ozawa, 2007). Some, finally, identify nacellids as a paraphyletic group (Yoon & Kim, 2007).

Nacella species are characterized by shell microstructures that include an 'irregular spherulitic prismatic structure type-A' M+2 layer and a 'regularly foliated' M+1 shell layer dorsal to the myostracum, an 'irregular complex crossed foliated structure' M-1 layer ventral to the myostracum, and an absence of crossed lamellar layers [terminology of Fuchigami & Sasaki (2005); see also MacClintock (1967) and Lindberg (1988, 1998)]. Most other patellogastropods from western South America lack foliated layers, e.g., the Lottiidae Gray, 1840, including *Lottia* and *Scurria* (Lindberg, 1988, 1998; Espoz et al., 2004). The nacellid genus, *Cellana*, represented in Peru and Chile by one Pliocene species (Herm, 1969; DeVries, unpublished data), has a prismatic M+3 and foliated M+2 layer, but also has crossed lamellar structures in layers M+1 and M-1 (MacClintock, 1967; Lindberg & Hickman, 1986; Fuchigami & Sasaki, 2005). The new species of *Nacella* described herein have clearly visible prismatic structure in their M+2 layer, foliation in their M+1 layer and lack crossed lamellar layers.

Subgenus *Nacella* Schumacher, 1817

Description: Shell very thin, apex very close to anterior end (Powell, 1973).

Nacella (*Nacella*) *lacrima*, sp. nov.

Figures 3–15

Diagnosis: Shell height extremely low. Aperture tear shaped. Radial sculpture of 60 ribs, differentiated by size posteriorly, sometimes obsolete.

Description: Shell conical, very thin, length under 30 mm; height extremely low (L:H ratio about 5:1 to 8:1). Aperture tear shaped: broadly elliptical posteriorly, rapidly narrowing and linear anteriorly, sharply rounded at anterior end. Shell margin planar, periphery of margin evenly curved, not crenulated. Apex orthogonal to slightly obtuse, located one-eighth or less of length from anterior end. Steep anterior slope concave, straight, or convex; posterior slope slightly convex; lateral slopes planar. Radial sculpture of up to 60 very low rounded ribs, often fewer in juveniles, obsolete in some adults; ribs not corrugated. Differentiation of primary and secondary ribs posteriorly, if present; rare secondary ribs inserted close to apex. Concentric sculpture of fine growth lines and irregular weak growth rugae. Coloring of concentric brown mottling. Interior with smooth or weakly radially striated intermediate area; central area broad and extending 80 percent of shell length.



Figures 3–15. *Nacella (Nacella) lacrima*, sp. nov. All are paratypes except holotype. DV 1279-1. Late early Pliocene.

Figure 3. MUSM INV 177. Dorsal view. Length is 17.3 mm.

Figure 4. MUSM INV 179. Dorsal view. Length is 15.4 mm.

Figure 5. MUSM INV 179. Ventral view.

Figure 6. MUSM INV 177. Ventral view. Angular pitting is from contact with sand grains.

Figure 7. MUSM INV 176. Dorsal view. Length is 25.0 mm.

Figure 8. MUSM INV 176. Ventral view.

Figure 9. UWBM 98627, holotype. Dorsal view. Length is 21.8 mm.

Figure 10. UWBM 98626. Close-up of regular foliated M + 1 layer (right) and prismatic M + 2 layer (left). Length of image is 7.4 mm.

Figure 11. UWBM 98621. Lateral view, anterior to left. Length is 9.7 mm.

Figure 12. MUSM INV 176. Lateral view, anterior to left.

Figure 13. UWBM 98620. Dorsal view. Length is 24.0 mm.

Figure 14. UWBM 98621. Dorsal view.

Figure 15. UWBM 98621. Ventral view.

Discussion: The extreme anterior position of the apex places this taxon in *Nacella (Nacella)*. The only other South American species in this subgenus, the Recent *N. (Nacella) mytilina*, lives throughout the Magellanic Province (Valdovinos & R  th, 2005). Its specimens are

laterally compressed, deeply arched, and have a radial sculpture of weak wrinkles. *Nacella (Nacella) kerguelensis* (E. A. Smith, 1877), a Recent species from the southern Indian Ocean (about 49  S), is nearly three times longer than *N. (Nacella) lacrima*, has a high

profile, and is not laterally compressed (Powell, 1973; Ubaldi, 1985a; note that images of *N. kerguelensis* differ in the two references).

Etymology: Latin 'lacrima,' meaning 'tear,' referring to the teardrop shape of this species.

Type Locality: DV 1279-1, base of southeast wall of sand-and-gravel quarry along the Pan-American Highway, five km (straight distance) from village of Ocoña (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel (Figures 2A–2C). 16°25'28"S, 73°09'14"W.

Material (all specimens from DV 1279-1, late early Pliocene; all but holotype are paratypes): MUSM INV 176, L 25.0, W 21.0, H 4.6; MUSM INV 177, L (17.3), W 13.9, H 2.2; MUSM INV 178, L 18.3, W 13.8, H 3.0; MUSM INV 179, L 15.4, W 12.0, H 2.5; UWBM 98619, L 24.8, W 21.7, H 4.3; UWBM 98620, L 24.0, W 17.1, H 3.0; UWBM 98621, L 9.7, W 7.6, H 1.9; UWBM 98622, L (7.8); UWBM 98623, holotype, L 21.8, W 16.0, H 3.9; UWBM 98624, L (7.1).

Occurrence: Late early Pliocene: southern Peru.

Subgenus *Patinigera* Dall, 1905

Type species: *Patella magellanica* Gmelin, 1791. Recent, southern South America.

Description: Shell more solid than *Nacella* (*Nacella*); apex closer to a central position (Powell, 1973).

Nacella (*Patinigera*) *oblea*, sp. nov.

Figures 16–26

Diagnosis: Shell very thin, height very low. Aperture nearly circular posteriorly; apex one-third of length from anterior. Radial sculpture of nearly 80 low ribs, usually with pronounced differentiation by size.

Description: Shell conical, very thin, length to about 40 mm; height very low (adult L:H ratio about 5:1). Aperture nearly circular posteriorly, broadly oval and slightly constricted anteriorly. Shell margin planar to slightly arched longitudinally, evenly curved with fine crenulations corresponding to primary ribs. Apex obtuse, located one-third of length from anterior end. Anterior slope usually planar, lateral and posterior slopes slightly convex. Radial sculpture of about 80 fine, low, rounded ribs near margin, including frequent distal insertions of secondary ribs; differentiation of primary and secondary ribs usually pronounced. Concentric sculpture of closely spaced, finely crenulated growth lines and irregularly spaced coarser growth rugae. Color uniformly cream. Interior faintly irides-

cent, intermediate area with fine radial striae and ridges; central area 60 to 80 percent of shell length.

Discussion: Specimens of *Nacella oblea* greatly resemble those of *N. clypeater* (Figures 27, 28), differing principally in being thinner, having an anterior end that is more constricted, primary and secondary ribs that are more differentiated, and a uniformly cream color. One specimen from 37 meters (Unit II) in the Huacclaco section (Figure 25) has a less constricted anterior, subdued to obsolete radial sculpture, and a purple-brown exterior like specimens of modern *N. clypeater*. Upper Pliocene Huacclaco specimens from 48 meters (Unit III) and 68 meters (Unit IV) (UWBM 98684, UWBM 98685, respectively) are thicker and the unworn specimen from Unit III has coarser radial sculpture than lower Pliocene specimens, characters that may indicate a transition had begun to typical *N. clypeater*.

Nacella clypeater is the only Recent western South American *Nacella* to occur north of the Magellanic Province (Valdovinos & R  th, 2005), ranging as far north as Arica, Chile (about 18°30'S) (Ram  rez-B  hme, 1996) and Atico, southern Peru (about 16°12'S); almost certainly it is not found as far north as Lima or north-central Peru, as claimed by Ubaldi (1985b) (A. Indacochea, V. Mogollon, written communication, 2008). *Nacella clypeater* differs from Magellanic *Nacella* by favoring subtidal habitats, especially the 'fondos blanqueados' described in V  squez & Vega (2004), expanses of subtidal substrate covered with white coralline algae (Meneses, 1993; Valdovinos, written communication, 2008). The great numbers of *N. clypeater* that congregate on the coralline blankets are usually encrusted with the algae. Oddly, though, Peruvian Pliocene specimens of *N. oblea* are entirely free of coralline encrustations, having only rare attachment scars from barnacles or *Scurria* limpets (Figure 24).

Etymology: Spanish 'oblea,' a Roman Catholic communion wafer, which this species resembles.

Type Locality: DV 1254, Huacclaco, ten km southeast of Chala along the Pan-American Highway, about 37 m in measured section (DV 1254-2; Figure 1). 15°53'25"S, 74°09'52"W.

Material (specimens are paratypes from DV 1254-2 and early late Pliocene unless otherwise stated): MUSM INV 180, DV 1254-bal6, L 38.2, W 31.7, H 7.2; MUSM INV 181, L 27.8, W 23.6, H 4.9; MUSM INV 182, L 29.3, W 25.4, H 5.2; MUSM INV 183, L (27.0), W 25.3, H 5.9; UWBM 98625, holotype, L 35.7, W 31.7, H 7.2; UWBM 98626, DV 1254-bal6, L 25.8, W 23.3, H 5.4; UWBM 98627, L (20.3); UWBM 98628, L 30.0, W 25.5, H (4.0); UWBM 98629, L 28.5, W 25.8, H 4.8; UWBM 98630, L 15.0, W 8.1, H 2.5; UWBM 98631,



Figures 16–26. *Nacella (Patinigera) oblea*, sp. nov. All paratypes except holotype.

Figure 16. UWBM 98629. DV 1254-2. Early late Pliocene. Dorsal view. Length is 28.5 mm.

Figure 17. MUSM INV 182. DV 1254-2. Ventral view. Length is 29.3 mm.

Figure 18. UWBM 98627. DV 1254-2. Regular foliated microstructure, first-order folia of M + 1 layer adjacent to myostracum. Width of broadened anterior end of central area (lower right) is 7.8 mm.

Figure 19. MUSM INV 180. DV 1254-bal6. Early late Pliocene. Lateral view, anterior to left. Length is 38.2 mm.

Figure 20. UWBM 98626. DV 1254-bal6. Dorsal view. Length is 25.8 mm.

Figure 21. UWBM 98625, holotype. DV 1254-2. Dorsal view. Length is 35.7 mm.

Figure 22. MUSM INV 180. Dorsal view.

Figure 23. MUSM INV 181. DV 1254-2. Lateral view, anterior to left. Length is 27.8 mm.

Figure 24. UWBM 98628. DV 1254-2. Dorsal view. Arrow points at *Scurria* scar. Length is 30.0 mm.

Figure 25. UWBM 98631, DV 1254-bal6. Dorsal view showing dark coloration (brown) near margin. Length is 34.6 mm.

Figure 26. UWBM 98625. Ventral view.

Figures 27, 28. *Nacella (Patinigera) clypeator* (Lesson, 1831). Pucatrihue, south-central Chile. Recent.

Figure 27. UWBM 98632. Dorsal view. Length is 38.0 mm.

Figure 28. UWBM 98633. Ventral view. Length is 43.3 mm.



Figures 29–39. *Nacella (Patinifera) intiforma*, sp. nov.

- Figure 29. UWB 98635, paratype. DV 1279-1. Late early Pliocene. Dorsal view, apex missing. Length is 33.1 mm.
 Figure 30. UWB 98635. Ventral view, central area missing.
 Figure 31. UWB 98637. DV 1267-1. Late early Pliocene. Dorsal view, posterior missing.
 Figure 32. UWB 98637. Close-up of microstructure: regular foliated M+1 layer and prismatic M+2 layer.
 Figure 33. UWB 98637. Close-up of microstructure: regular foliated M+1 layer and cross foliated M-1 layer.
 Figure 34. UWB 98636. DV 1267-1. Dorsal view. Length is 37.6 mm.
 Figure 35. UWB 98634, holotype. DV 1279-1. Dorsal view. Length is 26.6 mm.
 Figure 36. UWB 98634. Ventral view.
 Figure 37. MUSM 185, paratype. DV 1279-1. Dorsal view. Length is 22.0 mm.
 Figure 38. UWB 98635. Lateral view, anterior to left.
 Figure 39. UWB 98634. Lateral view, anterior to left.

DV 1254-bal6, L 34.6, W 30.3, H 7.0; UWB 98684, DV 1254-10, late Pliocene, L 43.2, W 41.3, H 11.1; UWB 98685, DV 1941-1, latest Pliocene, L 43.9, W 38.4, H 11.2.

Occurrence: Early late Pliocene: southern Peru.

Nacella (Patinigera) intiforma, sp. nov.

Figures 29–39, 46

Diagnosis: Shell moderately thin; height very low. Aperture elliptically quadrate; aperture one-third of length from anterior. Radial sculpture of about 55 to

60 strong corrugated ribs, usually alternatingly differentiated by size anteriorly and posteriorly.

Description: Shell conical, moderately thin, length to about 60 mm; height very low (L:H ratio about 4:1 to 6:1). Aperture elliptically quadrate, broader posteriorly. Shell margin planar to slightly arched longitudinally, evenly curved with crenulations corresponding to ribs. Apex obtuse, located one-quarter of length from anterior end. Anterior slope steep, planar to slightly concave, posterior slope slightly convex, lateral slopes planar. Radial sculpture of about 55 to 60 ribs, differentiated by size anteriorly and posteriorly, some-

times laterally. Ribs weakly to strongly corrugated by intersections with strong concentric growth lines; corrugations somewhat irregular and not always evenly sized or spaced. Interior faintly iridescent; interior margin crenulated; central area 60 to 80 percent of shell length.

Discussion: Specimens of *Nacella intiforma* have a shape similar to those of *N. oconaensis*, sp. nov. (see below), but primary ribs of the latter species are fewer and coarser. Specimens of *N. intiforma* resemble small deep-water nacellids assigned by Powell (1973) to *N. (Patinigera) deaurata* form *delicatissima* (Strebel, 1907), which have equally low profiles (but see Valdovinos & R  th (2005) for statistics on higher profiles) and equally strong ribs, albeit fewer. Also similar are specimens of the strongly ribbed *N. (Patinigera) terroris* (Filhol, 1880), which are found only on sub-Antarctic Campbell Island (52  32S, 169  09'E), near New Zealand, but these have a more centrally located apex, a much higher profile (L:H ratio about 2:1 to 3:1) and are less elongate.

Specimens similar to those of *N. intiforma* were found in early late Pliocene bioclastic deposits of the Huacallaco section (DV 1254-bal6). Ribs on the larger specimen (UWBM 98643; L 46 mm) are worn, but present in sufficient number for it to be assigned to *N. intiforma*. The anterior, posterior, and lateral slopes of the specimen are convex, but slopes closer to the apex are planar. A 30-mm long Pliocene specimen of *Nacella* was reported from south-central Chile (Le Roux et al., 2008). Photographs provided by S. Nielsen (written communication, April, 2008) reveal an apertural form, height, and nearly obsolete sculpture similar to that of the large Huacallaco example of *N. intiforma*.

Etymology: Quechua 'inti,' meaning sun, referring to the well formed ribs that produce a sunburst pattern on this species.

Type Locality: DV 1279-1, base of southeast face of sand-and-gravel quarry along the Pan-American Highway, 5 km (straight distance) from village of Oco  a (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel (Figures 2A–2C). 16  25'28"S, 73  09'14"W.

Material (all specimens late early Pliocene): MUSM INV 184, DV 1279-1, paratype, L 20.9, W 13.8, H 3.3; MUSM INV 185, DV 1279-1, paratype, L 22.0, W 14.8, H (3.7); MUSM INV 186, DV 1267-1, L (25.9); UWBM 98634, DV 1279-1, holotype, L 26.6, W 18.6, H 4.8; UWBM 98635, DV 1279-1, paratype, L 33.1, W 22.6, H (5.5); UWBM 98636, DV 1267-1, L 37.6, W 27.7, H 9.2; UWBM 98637, DV 1267-1, L (35.2), W 35.8, H (9.0); UWBM 98638, DV 1045-1, L 60.4, W 46.0, H 8.1; UWBM 98643, DV 1254-bal6, L (46.3), W

38.7, H 10.4; UWBM 98644, DV 1254-bal6, L 23.1, W (17.0), H 4.0.

Occurrence: Late early Pliocene to early late Pliocene: southern Peru, south-central Chile.

Nacella (Patinigera) oconaensis, sp. nov.

Figures 40–45, 47, 48

Diagnosis: Shell thick, height low. Aperture elliptical to oval; apex one-third of length from anterior. Radial sculpture of about 30 to 40 strong but weakly corrugated ribs, usually differentiated by size laterally and posteriorly.

Description: Shell conical, moderately thick, length to about 50 mm; height low (H:L ratio 4:1 to 5:1). Aperture elliptical to oval, broader posteriorly. Shell margin evenly curved, sometimes deformed; longitudinally planar to arched; with crenulations corresponding to ribs. Apex obtuse, located one-quarter to one-third of length from anterior end. Anterior slope steepest, all adult slopes planar to slightly convex; break in slope separates more elevated juvenile stage. Radial sculpture of about 30 to 40 primary ribs, with insertion of secondary ribs posteriorly and laterally, generally not anteriorly. Ribs weakly corrugated at intersections with fine concentric growth line crenulations and coarser rugae. Interior margin crenulated; intermediate area smooth; central area about 60 to 80 percent of shell length.

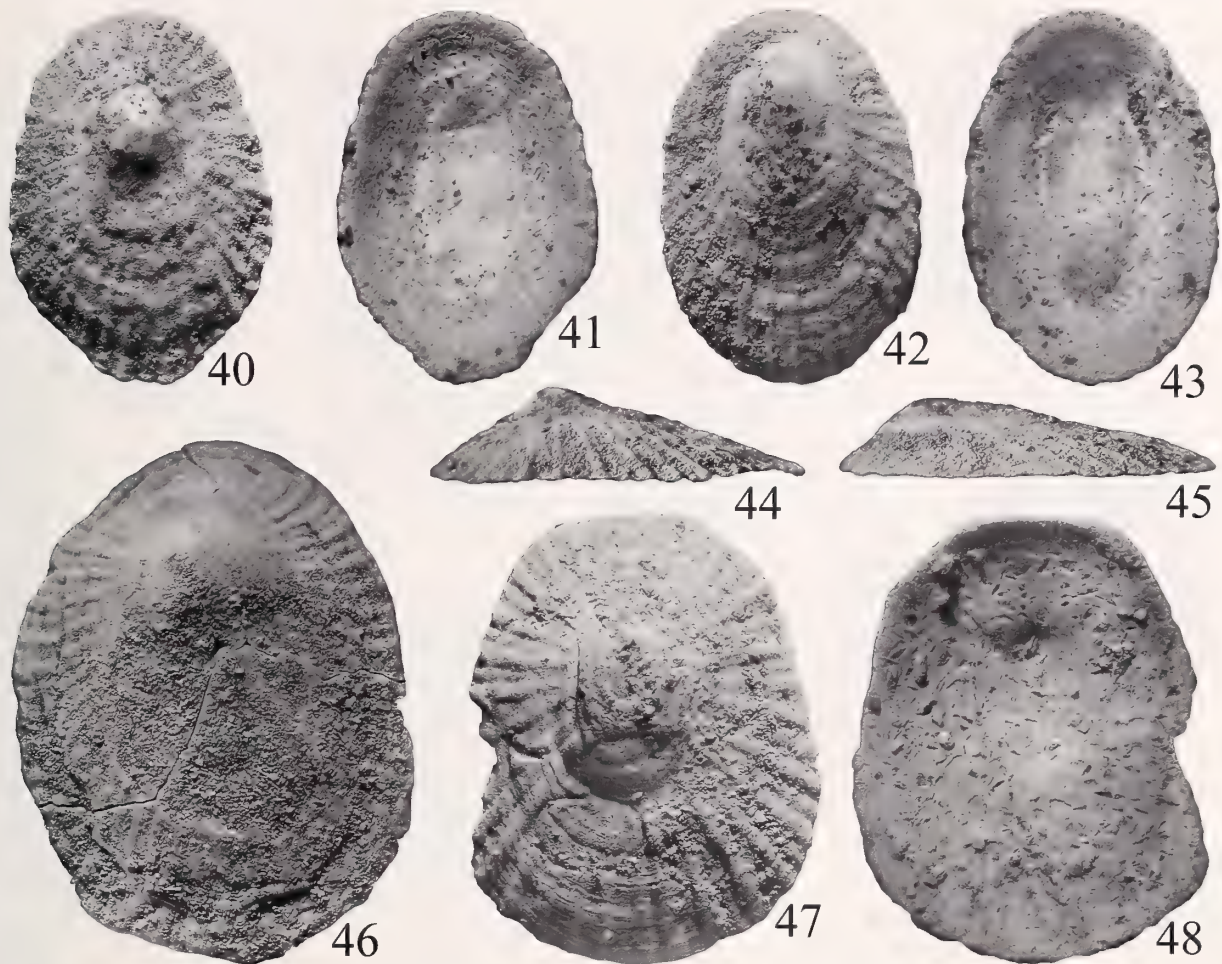
Discussion: Specimens of *Nacella (Patinigera) oconaensis* at the type locality (DV 1279-1) resemble those of *N. intiforma*, with which they occur, but they are thicker and have fewer and coarser ribs. Both taxa may be ecophenotypic variants of the same species.

The radial sculpture and rib number of *Nacella oconaensis* match those of extant *N. (Patinigera) macquariensis* Finlay, 1927, from Macquarie Island (54  30'S, 159  E) and Heard Island (53  S, 74  E) (Powell, 1973), but the latter species has a much higher profile (L:H ratio about 2:1).

Etymology: Named for Oco  a, a nearby village.

Type Locality: DV 1279-1, base of southeast face of sand-and-gravel quarry along the Pan-American Highway, 5 km (straight distance) from village of Oco  a (Figure 1). Limpets were found in finely bedded and cross-bedded fine-grained gravel. 16  25'28"S, 73  09'14"W.

Material (all localities except DV 1254-bal6 are late early Pliocene): MUSM INV 187, DV 1279-1, paratype, L 30.7, W 21.9, H 6.8; MUSM INV 188, DV 1254-bal6, early late Pliocene, L 19.9, W 12.5, H 3.7; UWBM 98639, DV 1279-1, holotype, L 29.7, W 20.6, H 5.5; UWBM 98640, DV 1279-1, paratype, L 17.9, W



Figures 40–45, 47, 48. *Nacella (Patinifera) oconaensis*, sp. nov.

Figure 40. MUSM INV 187, paratype. DV 1279-1. Late early Pliocene. Dorsal view. Length is 30.7 mm.

Figure 41. MUSM INV 187. Ventral view.

Figure 42. UWBW 98639, holotype. DV 1279-1. Dorsal view. Length is 29.7 mm.

Figure 43. UWBW 98639. Ventral view.

Figure 44. MUSM INV 187. Lateral view, anterior to left.

Figure 45. UWBW 98639. Lateral view, anterior to left.

Figure 46. *Nacella (Patinifera) intiforma*, sp. nov. UWBW 98638. DV 1045-1, late early Pliocene. Dorsal view showing growth line scars and deformed aperture. Length is 60.4 mm.

Figure 47. UWBW 98641, paratype. DV 1279-1. Dorsal view, showing deformed aperture and six scars from epibiotic limpet, *Scurria*. Length is 28.6 mm.

Figure 48. UWBW 98641. Ventral view.

13.1, H 3.9; UWBW 98641, DV 1279-1, paratype, L 28.6, W 22.5, H 6.5.

Occurrence: Late early Pliocene to early late Pliocene; southern Peru.

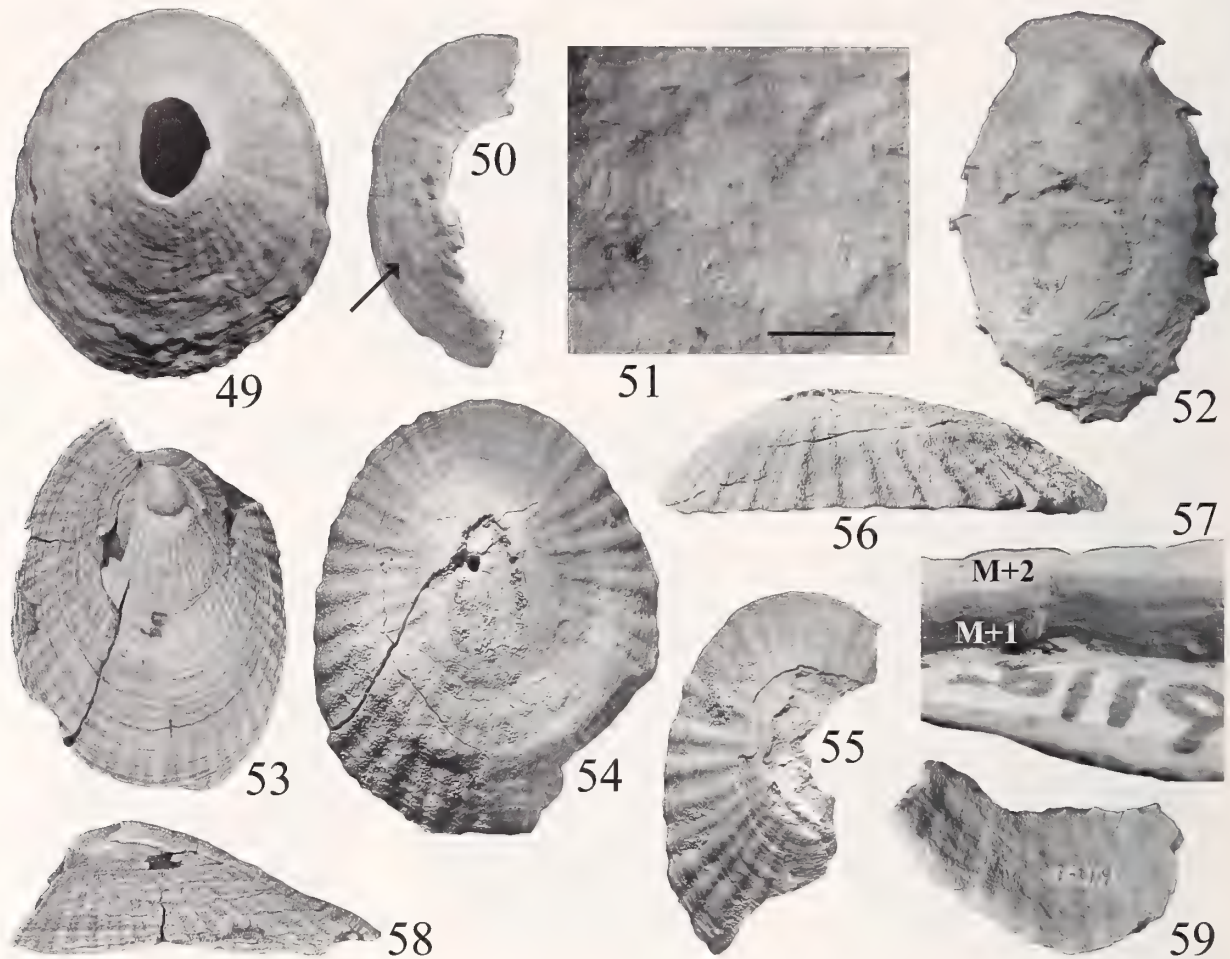
Nacella (Patinifera) chalaensis, sp. nov.

Figures 49, 50

Diagnosis: Shell broadly oval. Apex located two-fifths of length from anterior end. Radial sculpture of about

45 weakly nodular ribs; secondary ribs absent or barely differentiated by size.

Description: Shell conical, estimated length to 50 mm, height low (L:H ratio about 4:1). Aperture broadly oval, slightly constricted anteriorly. Shell margin planar to arched longitudinally, evenly curved with weak crenulations corresponding to coarsest ribs. Apex obtuse, located two-fifths of length from anterior end. Anterior and posterior slopes planar, lateral slopes slightly convex. Radial sculpture of about 45 low



Figures 49, 50. *Nacella (Patinigera) chalaensis*, sp. nov. Late early Pliocene.

Figure 49. UWB 98686, holotype. Dorsal view. Length is 40.0 mm.

Figure 50. UWB 98642, paratype. Dorsal view, fragment. Arrow points at *Scurria* scar. Length is 46.4 mm.

Figures 51, 52. *Nacella (Patinigera)* sp. indet. UWB 98687. Early late Pliocene.

Figure 51. Foliated M-1 layer, ventral surface of central area. Scale bar is 1 mm.

Figure 52. Dorsal view, central area. Length is 66.2 mm.

Figures 53, 58. *Nacella (Patinigera) nielsenii*, sp. nov. WM 10612, holotype. Chiloé, southern Chile. Late early Miocene.

Figure 53. Dorsal view. Length is about 35 mm.

Figure 58. Lateral view, anterior to left.

Figures 54-57, 59. *Nacella (Patinigera) reichae*, sp. nov.

Figure 54. UWB 98645, holotype. DV 611a-1. Late Oligocene. Dorsal view. Length is 54.3 mm.

Figure 55. MUSM 189, paratype. DV 638-1. Late Oligocene. Dorsal view, right side and posterior missing. Length is 48.5 mm.

Figure 56. UWB 98645. Lateral view, anterior to left.

Figure 57. UWB 98645. Close-up of prismatic M+2 outermost layer and regular foliated M+1 layer.

Figure 59. UWB 98647. DV 611a-1. Ventral view showing weak internal ribbing. Width is 32.0 mm.

rounded primary ribs, all variably nodose, fading towards margin. Secondary ribs absent or negligibly differentiated from primary ribs. Concentric sculpture of regularly spaced growth lines accentuating nodes and irregularly spaced growth breaks. Color cream proximal to apex, pale brown distally. Interior with weakly developed radial ribs; central area missing.

Discussion: Specimens of *Nacella chalaensis* are nearly

as broadly oval as those of the late Pliocene *N. oblea* and modern *N. clypeator*, but the ribs are fewer, broader, and weakly nodose; they are also broader anteriorly than all but deformed specimens of *N. intiforma* and *N. oconaensis*; the former has many more ribs, whereas the latter has a number equal to that of *N. chalaensis*. Additional material may reveal that morphological continua exist amongst specimens of *N. chalaensis*, *N. oconaensis* and *N. intiforma*.

Specimens of *Nacella chalaensis* from Unit I are the oldest from Huacllaco. They are assigned a late early Pliocene age based on associated mollusks (*Acanthina triangularis* DeVries, 2003; *Concholepas kieneri* Hupé, 1854; *Xanthochorus eripepomis* DeVries, 2005) (DeVries, 1995, 2003, 2005).

Etymology: Named for the nearby town of Chala.

Type Locality: DV 1628, Huacllaco, ten km southeast of Chala along the Pan-American Highway, less than 5 meters above the transition from orange sandstones of the Pisco Formation to balanid coquina of the La Planchada Formation (DV 1628-1; Figure 1). 15°53'25"S, 74°09'52"W.

Material: UWBM 98686, DV 1628-1, holotype, late early Pliocene, L 40.0, W 33.8, H 8.4; UWBM 98642, DV 1628-1, paratype, L (46.4).

Occurrence: Late early Pliocene: southern Peru.

Nacella (Patinigera), sp. indet.

Figures 51, 52

Discussion: Two incomplete specimens of *Nacella*, one with a central area exceeding 66 mm in length, were discovered in 2008 by Liz Nesbitt (Burke Museum of Natural History and Culture, University of Washington, USA) in talus from basal beds of Unit III at Huacllaco. The estimated length of the largest specimen is 80–90 mm, larger than any other fossil or modern *Nacella*, excepting *N. (Nacella) kerguelensis*. The foliated M–1 layer (Figure 51) distinguishes the Huacllaco specimens from Peruvian and Chilean Pliocene specimens of *Cellana fuenzalidai* (Herm, 1969). The apex, located about one-quarter to one-third of the length from the anterior, indicates an assignment to *N. (Patinigera)* rather than *N. (Nacella)*.

Material (all specimens from Huacllaco (DV 1929-1, early late Pliocene): UWBM 98687, L (66.2), W (42.5); UWBM 98688, L (44.9), W (29.8); UWBM 98689, L (66.3).

Occurrence: Early late Pliocene: southern Peru.

Nacella (Patinigera) nielsenii, sp. nov.

Figures 53, 58

Patinigera aff. *terroris* (Filhol). Fleming, in Watters & Fleming, 1972, p. 390, pl. 28, fig. 6a.

Diagnosis: Shell with high profile. Apex recurved, about one-sixth of length from anterior end. Radial sculpture of about 55 strong corrugated ribs.

Description: Shell conical, moderately thick, length

about 40 mm; moderately high profile (L:H ratio 3:1). Aperture ovate, broader posteriorly. Shell margin evenly curved, with crenulations corresponding to ribs. Apex recurved, located one-sixth length from anterior end. Anterior slope steepest, planar below recurved apex; posterior slope planar. Radial sculpture of 56 strong, broadly rounded, corrugated ribs, with secondary ribs sometimes formed laterally from interspaces. Corrugations at intersections with strong concentric growth lines; concentric growth rugae also present. Interior unknown.

Discussion: A single nacellid specimen was collected on the west coast of Chiloé, Chile (42°S) by Watters & Fleming (1972). Fleming referred this limpet and other mollusks from Chiloé to the Pliocene, but the co-occurrence of *Acanthina katzi* (Fleming, 1972) and *Testallium cepa* (Sowerby, 1846) [misidentified as '*Chorus* aff. *blainvillei* (d'Orbigny)' by Fleming; see DeVries (1997) and Vermeij & DeVries (1997)] indicates an age between latest Oligocene and early middle Miocene (DeVries, 2003; DeVries & Frassinetti, 2003). The presence of the venerid bivalve *Amiantis* Carpenter, 1884, is not evidence for a Pliocene age, as was inferred by Fleming, because the genus, in addition to being represented by *A. domeykoana* (Philippi, 1887) in Pliocene beds from Chile (Philippi, 1887; Herm, 1969) and southern Peru (Muizon & DeVries, 1985), also occurs in lower Miocene to upper Miocene deposits of southern Peru (DeVries, unpublished data). Recent ⁸⁷Sr/⁸⁶Sr isotopic analyses of shell material from *A. katzi* and *Lamprodomina dimidiata* (Sowerby, 1846) from western Chiloé have yielded ages of about 16 to 19 Ma (Nielsen & Golodny, 2006), consistent with molluscan biostratigraphic data (DeVries & Frassinetti, 2003). Hence, the single specimen of *N. nielsenii* is assigned a late early Miocene age.

The anterior position of the apex, fine corrugations and faded ribs across the posterior slope of *Nacella (Patinigera) nielsenii* recall specimens of *N. (Nacella) lacrima*, although the latter is extremely flattened and has an apex even farther anteriorward. The Chiloé specimen also resembles *N. (Nacella) kerguelensis*, which has an equally high profile but an apex also closer to the anterior end. Given its early Miocene age, its radial sculpture like that of *N. lacrima* and *N. kerguelensis*, and its apical position intermediate between species of *N. (Nacella)* and *N. (Patinigera)*, *N. nielsenii* may be the known *Nacella* closest to the evolutionary divergence of the two subgenera. Compared to its consubgenera, the modern *N. (Nacella) mytilina* appears to be a highly derived species with a loss of typical nacellid ribs and an acquired lateral compression unique for all *Nacella*.

Etymology: Named in recognition of Dr. Sven Nielsen

and his contributions to our knowledge of Cenozoic mollusks in Chile.

Type Locality: Locality E: “isolated stack, southeast side of Punta Ahuenco” (Fleming, in Watters & Fleming, 1972, p. 380). 42°06′29″S, 74°03′19″W (Google Earth).

Material: WM 10612, holotype, L 35, W 26, H 12.

Occurrence: Late early Miocene: Chiloé, southern Chile.

Nacella (Patinigera) reicheae, sp. nov.

Figures 54–57, 59

Diagnosis: Shell with low profile, apex about one-third of length from anterior end. Radial sculpture of about 35 strong and broadly rounded corrugated ribs.

Description: Shell conical, moderately thick, estimated length about 80 mm; height low (H:L ratio about 5:1). Aperture elliptical. Shell margin evenly curved, elevated postero-laterally, with crenulations corresponding to ribs. Apex obtuse, located one-third of length from anterior end. All slopes planar to convex. Radial sculpture of about 35 strong, broad rounded ribs, with interspaces only somewhat less wide, in some cases raised into a low secondary rib. Ribs finely corrugated by intersecting growth lines. Interior margin sometimes flattened, crenulated; intermediate area scored by broad grooves corresponding to exterior ribs; central area covered. Layers include prismatic M+2, prominent first-order foliation in M+1, and less well defined foliation in M–1.

Discussion: The outermost layer of *Nacella reicheae* has curved first-order crystals without sharply defined edges, consistent with the ‘irregularly spherulitic prismatic structure type-A’ of the M+2 layer in *Nacella* (Fuchigama & Sasaki, 2005). The underlying broad low-dipping folia match those in the ‘regularly foliated’ M+1 layer of *Nacella* (Figure 57). Short folia in packets at differing angles and oriented more steeply than those in the M+1 layer resemble ‘crossed foliated’ layers of Fuchigama & Sasaki (2005). No vertical crossed lamellar structures were observed, thereby precluding an assignment of this taxon to *Cellana* or any genus of Lottiidae (MacClintock, 1967; Lindberg, 1988, 1998; Fuchigama & Sasaki, 2005).

All specimens of *Nacella reicheae* were found near Cerro Poroma in several meters of bioclastic sandstone and gravel blanketing a fissure-riddled peneplain carved from upper Cretaceous plutonic rocks. The seaward-sloping erosional surface is a product of the late Eocene Incaic Orogeny (Noble et al., 1979b). Overlying continental volcanoclastic sediments of the

Nazca Group contain intercalated ash beds dated at 18 to 23 Ma (Noble et al., 1979a).

The presence of *Turritella woodsi* Lisson, 1925, led Rivera (1957) to assign an Eocene age to the Poroma molluscan fauna, but the range of *T. woodsi* is now properly understood to be latest Eocene (Otuma Formation) to early Miocene (lower Chilcatay Formation) (DeVries, 1998; DeVries et al., 2006). The additional occurrence in the Poroma beds of *Testallium cepa*, misidentified as *Peruficus* Olsson, 1932, in more southerly 25-Ma deposits (Noble et al., 1985; DeVries, 2001a) that were also mis-assigned to the Eocene by Petersen (1954) and Pecho (1983), indicates a latest Oligocene to early middle Miocene age for the *Nacella*-bearing beds (Vermeij & DeVries, 1997; DeVries & Frassinetti, 2003). A latest Oligocene age for the Poroma specimens of *Nacella reicheae* is proposed, it being consistent with molluscan ranges, ⁴⁰K–⁴⁰Ar dates, and the presumed synchronicity of a latest Oligocene transgressive event across the coastal margin of southern Peru (DeVries, 1998, 2001a).

The two largest specimens attributed to *Nacella reicheae* (UWBM 98646, UWBM 98650) are partially and poorly preserved. That they are patellogastropods and nacellids is without doubt, since one exhibits a continuous shell layer across the apex and both have a well developed foliated M+1 layer and prismatic M+2 layer. The high profile of one specimen and coarse radial sculpture of both specimens, however, may be evidence that a second species of Oligocene *Nacella* occupied the Poroma peneplain, thereby implying that the southern Peruvian coast may have been populated by a diverse but poorly preserved *Nacella* fauna since at least 25 Ma.

Etymology: Named in honor of the late Dra. Maria Reiche, who dedicated 50 yr to the study and preservation of the nearby Nazca lines.

Type Locality: DV 611a-1, midpoint of the northwestern flank of Cerro Poroma (Figure 1), at the contact between crystalline basement rock and an overlying sedimentary sequence (Figure 2F). 14°59′58″S, 74°59′08″W (Google Earth).

Material (all specimens late Oligocene; all specimens paratypes except holotype): MUSM INV 189, DV 638-1, L (48.5), H (10.7); UWBM 98645, DV 611a-1, holotype, L 54.3, W 42.4, H 11.9; UWBM 98646, DV 611a-1, L (62.4); UWBM 98647, DV 611a-1, W (37.2); UWBM 98648, DV 611a-1, W (32.0); UWBM 98649, DV 638-1, W (36.8); UWBM 98650, DV 471-1, L (66.0), W (55.2), H (22.5).

Occurrence: Late Oligocene: southern Peru.

DISCUSSION

Biogeographic constraints on Pliocene *Nacella*

Most modern limpets in temperate waters between Chiloé (42°S) and Trujillo (8°S), i.e., the Peruvian Faunal Province, are species of *Fissurella* (Vetigastropoda: Fissurellidae) or *Scurria* (Patellogastropoda: Lottiidae) (McLean, 1984; Alamo & Valdivieso, 1997; Espoz et al., 2004). Modern mean annual SSTs in this region range between 14°C and 20°C. Most modern limpets from Pacific shores of the Magellanic Faunal Province (Chiloé to Cape Horn) belong to the genera *Fissurella*, *Scurria*, and *Nacella*. These limpets experience mean annual SSTs between 7°C and 14°C. *Nacella* from Antarctica, the Scotia Arc, and Heard, Kerguelen, Macquarie, and Campbell Islands endure mean annual SSTs under 8°C. Such data would imply that *Nacella* is a cold-water genus (Powell, 1973; Lindberg, 1988; Nakano and Ozawa, 2007), excepting only the Chilean *N. (Patinigera) clypeator*, which ranges north (Ramírez-Böhme, 1996; Valdovinos & Rüth, 2005; A. Indacochea and V. Mogollon, written communications, 2008) into waters with a mean annual SST of up to 19°C.

Pliocene limpets of southern Peru belong to *Fissurella* (DeVries, 2008), *Nacella*, and *Scurria* (recognized from epibiotic scars on *Fissurella* and *Nacella*; see Figures 24, 47 and 50). The presence of at least five *Nacella* species at 16°S, representing both *N. (Nacella)* and *N. (Patinigera)*, challenges the idea that *Nacella* is an obligate cold-water taxon. Typical modern seasonal SSTs along the southern Peruvian margin range between 14°C (winter) and 22°C (summer) (Instituto del Mar del Perú; http://200.60.133.147/uprsig/sst_prov.html; April, 2008). Pliocene SSTs are likely to have been warmer, inasmuch as the early Pliocene and even late Pliocene global ocean and atmosphere were warmer than at present (Zachos et al., 1996; Dowsett et al., 1999; Ravelo et al., 2004). The presence of warm-water molluscan taxa in southern Peru and Chile during the early Pliocene [e.g., *Dosinia ponderosa* (Schumacher, 1817), *Chionopsis* sp., *Protothaca asperima* (Sowerby, 1835), *Northia* sp., *Terebra* sp., and *Cancellaria* spp. (Herm, 1969; Muizon & DeVries, 1985; DeVries, 2001b, unpublished data) and their absence since the late Pliocene further indicates warmer SSTs prevailed while Pliocene *Nacella* occupied southern Peruvian shores.

With Pliocene *Nacella* so successful in warm waters at tropical latitudes, a reason unrelated to SSTs is needed to explain their presence in southern Peru, e.g., a paleogeographic reason. Modern *Nacella* are most diverse in Magellanic fjords, the consequence, Valdovinos & Rüth (2005) speculated, of habitat fragmentation during Pleistocene cycles of eustatic sea-level change. Fjords would also afford *Nacella* protection

from the most energetic waves of the Pacific Ocean. Such protection does influence the distribution of modern *Nacella*. Chilean species with high shells and strong pedal muscles live in exposed intertidal settings, while those with low thin shells and small pedal muscles inhabit quieter subtidal environments (Valdovinos & Rüth, 2005; but note the low profile of *N. clypeator* specimens from exposed beaches at Pucatrihue, south-central Chile; UWB 98632, 98633). Similar distributional patterns have been observed for sub-Antarctic populations of *N. concinna* (Beaumont & Wei, 1991; Nolan, 1991) and *N. macquariensis* (Simpson, 1985) and Argentinean populations of *N. deaurata* (Morriconi & Calvo, 1993).

Protected paleo-embayments with sand and cobble substrates could have provided Pliocene Peruvian *Nacella* with quiet waters near Acari, Aguada de Lomas, and Nazca (Muizon & DeVries, 1985; DeVries, 1988). Of these embayments, however, only the largest, near Nazca, has yielded a limpet: a massive *Lithophaga*-bored *Cellana fuenzalidai* from the lee side of a Pliocene peninsula. The five Peruvian *Nacella*, in contrast, whose low profile might otherwise indicate life in a protected setting, lived along an exposed cliff-lined coast like that which has prevailed throughout the Quaternary. About three-quarters of the specimens from these five Pliocene species show break-and-repair scars along their present or former margins, a proportion comparable to those for exposed populations of *N. concinna* in the South Shetland Islands and *N. delesserti* (Philippi, 1849) on Marion Island and much less than that for a quiet-water population of *N. deaurata* from the Falkland Islands (Cadée, 1999). The Pliocene taxa of southern Peru, it seems, did live a life exposed to high-energy waves, a situation that persists today, although only one species of *Nacella* now lives there.

A change in the ecological landscape might explain the late Pliocene demise of Peruvian *Nacella*. Littoral molluscan faunas suffered a mass extinction during the late Pliocene (DeVries, 2001b), a time when patterns of competition for space and food would have been radically altered, as well as the interactions between a changing cast of predators and prey. Barnacles, for example, presently play a complex role in the settlement and success of modern keyhole limpets (Lopez et al., 1999). The dominance of barnacle species in southern Peru shifted considerably during the late Pliocene (DeVries, unpublished data), with possible impacts on the viability of *Nacella* populations. Coralline algae are an important food for some *Nacella* (Vásquez & Vega, 2004; Valdovinos, written communication, 2008), as are the fronds and spores of kelp (Blankley & Branch, 1985). Changes in their distribution could also explain the late Pliocene disappearance of Peruvian *Nacella*. In Antarctica, kelp gulls (*Larus*) prey heavily upon

intertidal *Nacella* (Branch, 1985; Cadée, 1999), as do fish (Blankley, 1982). Increased predation of intertidal organisms could have affected the survival of Peruvian *Nacella*. All of these hypotheses are plausible, but to date, none has been investigated.

Origin of *Nacella*

Molecular and morphological data show *Nacella* and *Cellana* share a common ancestor (e.g., Lindberg, 1988; Nakano & Ozawa, 2007). A southern origin for *Nacella* + *Cellana* (= Nacellidae) has been proposed (Koufopanou et al., 1999; Nakano & Ozawa, 2007) based on accounts of Eocene *Cellana* from Seymour Island, Antarctic Peninsula (Stillwell & Zinsmeister, 1992), New Zealand (Beu et al., 1990) and unconfirmed *Cellana* from Cretaceous beds of Australia (Powell, 1973). Nevertheless, the oldest fossils of *Cellana* verified by shell microstructure lived during the late Eocene in the northeastern Pacific Ocean (Lindberg & Hickman, 1986) and the oldest fossils of *Nacella*, likewise verified by shell microstructure, lived during the late Oligocene at tropical latitudes in Peru (this report). A Tethyan origin for Nacellidae is therefore a stronger possibility than when the idea was rejected by Koufopanou et al. (1999). Furthermore, the Pliocene history of *Nacella* in western South America is a cautionary tale for those who would invoke the modern diversity of austral *Nacella* as proof of a southern high-latitude origin. At least five Pliocene species of *Nacella* lived in southern Peru when its shores were bathed by water over 20°C. Their extinction by the end of the Pliocene produced a modern Weddellian distribution (*sensu* Zinsmeister, 1982) for the genus, but one of only relatively recent vintage.

Because of the Eocene age for the Oregonian *Cellana*, the timing for the evolutionary separation of *Nacella* and *Cellana* was set prior to 38 Ma by Koufopanou et al. (1999) and Goldstien et al. (2005). If, however, the shell microstructure of *Cellana* is plesiomorphic and if the complete loss of crossed lamellar microstructure in *Nacella* is a synapomorphy of *Nacella* alone, two possibilities raised by Koufopanou et al. (1999), then a clade of modern *Nacella* taxa could be a sister group to all modern *Cellana* but not to the group of Eocene + modern *Cellana*. *Cellana*, in other words, could be a paraphyletic group encompassing Eocene *Cellana*, modern *Cellana*, and all *Nacella*. If true, *Nacella* could have evolved more recently than 38 Ma. The discovery of a 25-Ma *Nacella* in southern Peru, however, limits how recently the *Cellana*/*Nacella* split could have occurred. With late Oligocene *Nacella* in Peru, early Miocene *Nacella* in Chile, and with South America a center of Pliocene and Quaternary *Nacella* diversity, it is possible that tropical

western South America was the region where the first *Nacella* appeared.

CONCLUSIONS

At least six new species of low-profile *Nacella* limpets from southern Peru, at least five Pliocene and one late Oligocene, and one *Nacella* from southern Chile, reassigned to the early Miocene, expand the record of this famously cold-water austral genus into tropical warmer-water latitudes of the southeastern Pacific Ocean. These taxa were collected from beds whose texture and sedimentary structures indicate high-energy littoral settings, although the low apex of most species suggests some moderation of that energy. The origin of *Nacella* remains a mystery, although these new accounts of *Nacella* establish that its present sub-Antarctic diversity does not exclude the possibility of an origin at lower latitudes, a possibility further strengthened by the presence of its nacellid sister group, *Cellana*, in the northern hemisphere during the late Eocene.

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APPENDIX

Locality-samples. 'GPS' refers to GPS field coordinates; 'GE' refers to coordinates from Google Earth imagery.

DV 471-1	Highlands of Cerro Poroma, four km east of Pan-American Highway, in bioclastic sandstone and gravel overlying crystalline basement (GE; 14°59'37"S, 74°58'30"W). Late Oligocene.
DV 611a-1	Mid-point of northwestern slopes of Cerro Poroma in bioclastic sandstone and gravel overlying crystalline basement (GE; 14°59'58"S, 74°59'08"W). Late Oligocene.
DV 638-1	Low ridges between Cerro Poroma and Callejon de Piedras, basal bioclastic sandstones above crystalline basement (15°01'53"S, 74°58'52"S). Late Oligocene.
DV 1045-1	Roadcuts along Pan-American Highway near La Planchada (GPS; 16°23'59"S, 73°12'43"W). Pliocene and Pleistocene.
DV 1254-2	Huacllaco, ten km southeast of Chala along Pan-American Highway, about 36–37 meters in measured section (GE; 15°53'16"S, 74°09'59"W). Late early Pliocene.
DV 1254-bal6	Huacllaco, ten km southeast of Chala along Pan-American Highway, 35–35.5 meters in measured section (GE; 15°53'16"S, 74°09'59"W). Late early Pliocene.
DV 1254-10	Huacllaco, ten km southeast of Chala along Pan-American Highway, 47–48 meters in measured section (GE; 15°53'15"S, 74°10'02"W). Early late Pliocene.
DV 1267-1	Roadcuts along Pan-American Highway near La Planchada; 15–20 meters of cross-bedded gravelly sandstone with wavy laminations of ash and scour-and-fill structures (GPS; 16°23'56"S, 73°12'30"W). Pliocene and Pleistocene.
DV 1279-1	Five km west-northwest of village of Ocoña along Pan-American Highway, base of sand-and-gravel quarry, southeast wall, in finely bedded cross-bedded gravel (GPS; 16°25'28"S, 73°09'14"W). Late early Pliocene.
DV 1628-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, bioclastic coquina in lowest five meters of measured section (GE; 15°53'25"S, 74°09'56"W). Late early Pliocene.
DV 1929-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, talus at base of slope on at about 39 meters in measured section (GE; 15°53'15"S, 74°10'01"W). Early late Pliocene.
DV 1941-1	Huacllaco, ten km southeast of Chala along Pan-American Highway, molds in former coquina at 68 m in measured section. (GE; 15°53'02"S, 74°10'07"W). Latest Pliocene.

A New Species of *Fissurella* from São Pedro e São Paulo Archipelago, Brazil (Vetigastropoda, Fissurellidae)

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Abstract. *Fissurella mesoatlantica* n. sp. is endemic to the Saint Peter and Saint Paul Archipelago, Brazil, located approximately in the middle Atlantic (00°55'N, 29°20'W). The species is very similar to *F. clenchi* from the mainland Brazilian coast, differing in having a taller, more richly sculptured shell and by anatomical details, such as the papillae of mantle border and epipodial tentacles. A complete anatomical description is included.

INTRODUCTION

The Arquipélago de São Pedro e São Paulo, or Saint Peter and Saint Paul Archipelago (ASPSP), is the remotest Brazilian oceanic set of islands. It is the tip of a huge oceanic mountain, with a base of approximately 4 by 2 km in size, its foot at 4 km depth, and an emerged tip of 13,000 m². The archipelago is located about 1,010 km off Calcanhar Cape, Rio Grande do Norte State, and about 870 km off Fernando de Noronha, the largest Brazilian oceanic archipelago; it is located approximately in the middle between Brazil and Africa, and close to the Equator line (Souza, 2007); the coordinates are 00°55'00"N 29°20'42"W.

The Archipelago is a strategic point for the Brazilian economy, as it ensures 238,000 km² of exclusive economic zone (Gonçalves, 2002). Since 1996, the Archipelago has continuously been occupied by 4-people research teams. Every person is allowed to work in that place only after an in-depth training, provided by the Brazilian Navy in its Rio Grande do Norte Base. Each team is allowed to work in 15-day expeditions.

Despite its biological importance, in being such an isolated place and an important source for the understanding of evolutionary and biological colonization, the local malacofauna has not been the main goal of any projects thus far. The few publications which deal with mollusks from ASPSP are restricted to species lists, with no thorough taxonomical research (e.g., Edwards & Lubbock, 1983, which listed four molluscan species). Even the more classic revision considering the malacofauna of the Brazilian oceanic islands, Leal (1991), did not include ASPSP.

A project supported by the federal Brazilian council of research (CNPq) permitted the collection and study of the ASPSP benthic invertebrate fauna. This paper deals with a common fissurellid in those islands, occurring intertidally, that turned out to be a new species after anatomical and taxonomical investiga-

tions. The species have been identified as *F. nubecula* (Linné, 1758) by Edwards & Lubbock (1983), which occurs in the northeastern Atlantic and Mediterranean. Additional data on the fissurellids see McLean (1984).

MATERIAL AND METHODS

The specimens were studied still alive, under a stereo-microscope, on board of Rebocador de Alto-Mar "Almirante Guilhem", commander Captain Antonio Cesar Portela Marques, Brazilian Navy. Later the specimens were preserved in 70% EtOH. The dissections were performed by standard techniques, with specimens immersed in preservative under a stereo-microscope. All drawings were done with the aid of a camera lucida. Most dissection steps were additionally digitally photographed. Radulae of five specimens were additionally examined by scanning electronic microscope (SEM) in the Laboratório de Microscopia Eletrônica of the Museu de Zoologia da Universidade de São Paulo (MZSP). For comparison with *Fissurella clenchi* Farfante, 1943, two lots of this species were examined anatomically: MZSP 80797 from Maceió, Alagoas, and MZSP 39965, from Santos, São Paulo. The data on the anatomy of *F. clenchi* and the further systematics of the Brazilian fissurellids are part of an ongoing project.

Anatomical abbreviations in the figures: **aa**, anterior aorta; **af**, afferent gill vessel; **an**, anus; **au**, auricle; **br**, subradular membrane; **bv**, blood vessel or sinus; **cc**, cerebral commissure; **ce**, cerebral ganglion; **co**, cerebro-pedal connective; **cv**, ctenidial vein or efferent gill vessel; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **eg**, esophageal gland or crop; **ep**, epipodium; **es**, esophagus; **ey**, eye; **fo**, foramen; **fs**, foot sole (mesopodium); **ft**, foot; **gf**, gastric fold; **gi**, gill; **gd**, gonoduct; **go**, gonad; **gs**, gill suspensory stalk; **ha**, head; **if**, inner fold of mantle border; **in**, intestine; **jw**, jaws; **ki**, kidney; **lm**, lateral muscle; **m1–m12**, odontophore muscles; **mb**,

mantle border; **mf**, middle fold of mantle border; **mj**, jaw and peribuccal muscles; **mo**, mouth; **mp**, mantle papillae; **mt**, mantle; **ne**, nephrostome; **nv**, nerve; **oc**, anterior odontophore cartilage; **od**, odontophore; **of**, outer fold of mantle border; **om**, ommatophore; **pc**, pericardium; **pg**, anterior furrow of pedal glands; **pl**, pedal-pleural ganglion; **pm**, pallial muscles; **ra**, radula; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sa**, gastric sorting area; **sc**, subradular cartilage; **se**, septum between odontophore and esophagus; **sm**, shell muscle; **sn**, snout; **sp**, gastric spiral caecum (vestigial); **st**, stomach; **sy**, statocyst; **te**, cephalic tentacle; **tg**, integument; **ve**, ventricle.

Abbreviations of institutions: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; BMNH, The Natural History Museum, London, UK; MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil; MORG, Museu Oceanográfico da Fundação Universidade de Rio Grande, RS, Brazil; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil.

SYSTEMATIC DESCRIPTION

Fissurella mesoatlantica new species

(Figures 1–40)

Fissurella (*Cremides*) *nubecula*: Edwards & Lubbock, 1983: 68 (*non* Linné, 1758).

Types: Holotype: MZSP 87462. Paratypes: BRAZIL. **São Pedro e São Paulo Archipelago;** Belmonte Island, 00°55'00"N 29°20'42"W (Simone & Cunha col.), east lagoon, MZSP 86568, 4 specimens, MZSP 86653, 1 specimen (7/xi/2007), Enseada, MZSP 86743, 15 specimens, ANSP A21718, 3 specimens, MNRJ 12476, 3 specimens, MZSP 86515, 2 shells (27/x/2007), MZSP 86518, 14 shells (28/x/2007), MZSP 86520, 9 shells (30/x/2007), MZSP 86528, 7 shells (31/x/2007), MZSP 86636, 7 shells (1/xi/2007), MZSP 87435, 2 shells (2/xi/2007), MZSP 86660, 1 shell (3/xi/2007), MZSP 86570, 9 specimens (4/xi/2007), MZSP 86575, 2 shells (9/xi/2007), northwestern coast, MZSP 86561, 29 specimens, MORG, 3 specimens, BMNH 20080492, 3 specimens (7/xi/2007), north coast, MZSP 86569, 19 specimens (7/xi/2007), canal with São Paulo Island, MZSP 86562, 14 specimens.

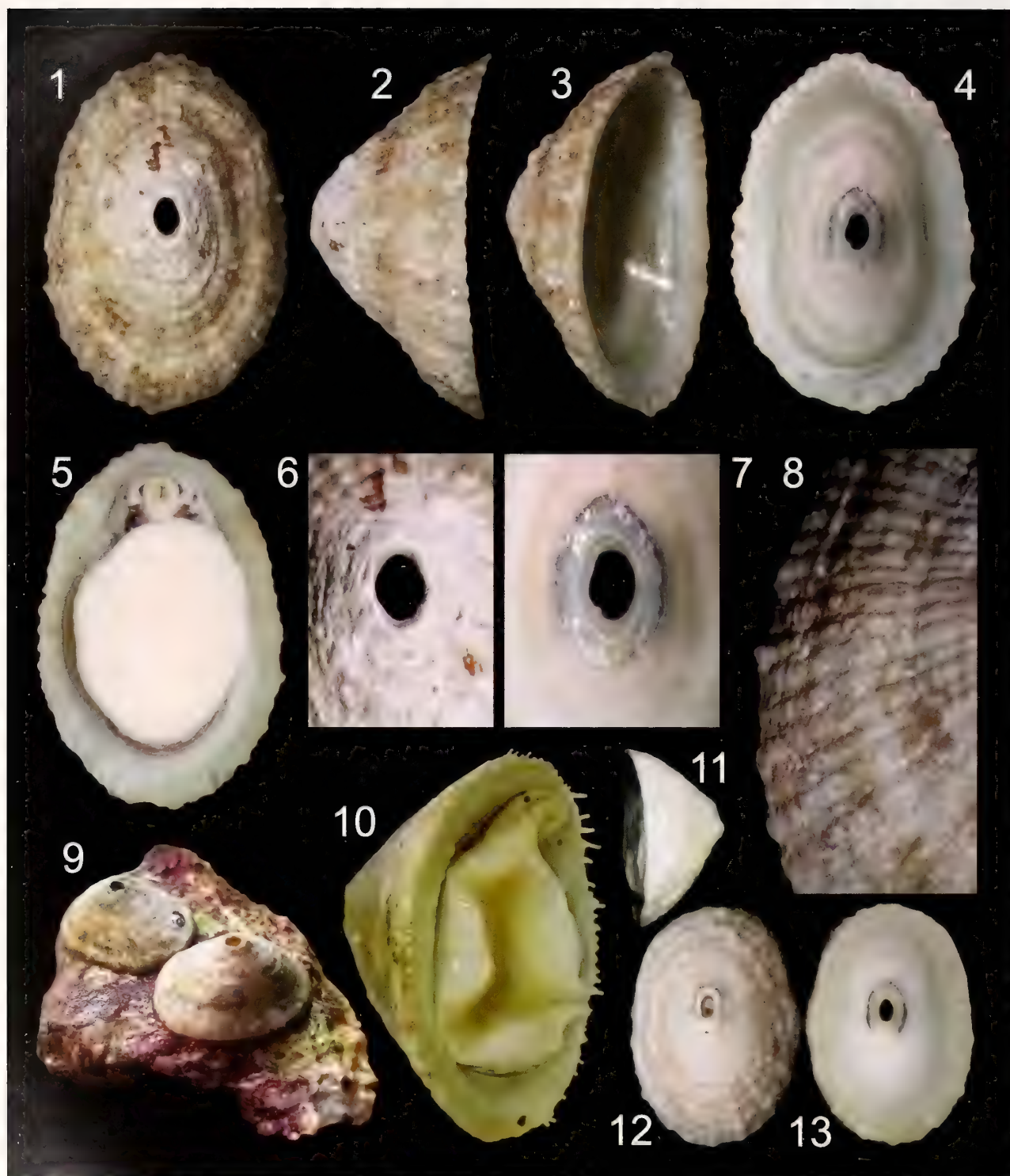
Type locality: BRAZIL. **São Pedro e São Paulo Archipelago;** Belmonte Island, Enseada, 00°55'01"N 29°20'44"W (Simone & Cunha col., 27/x/2007).

Diagnosis: Shell up to 20 mm; about half as high as long; foramen elliptical, central to anterior. Sculptured by about 50 radial, relatively tall ribs, with concentric nodes. Endemic from ASPSP.

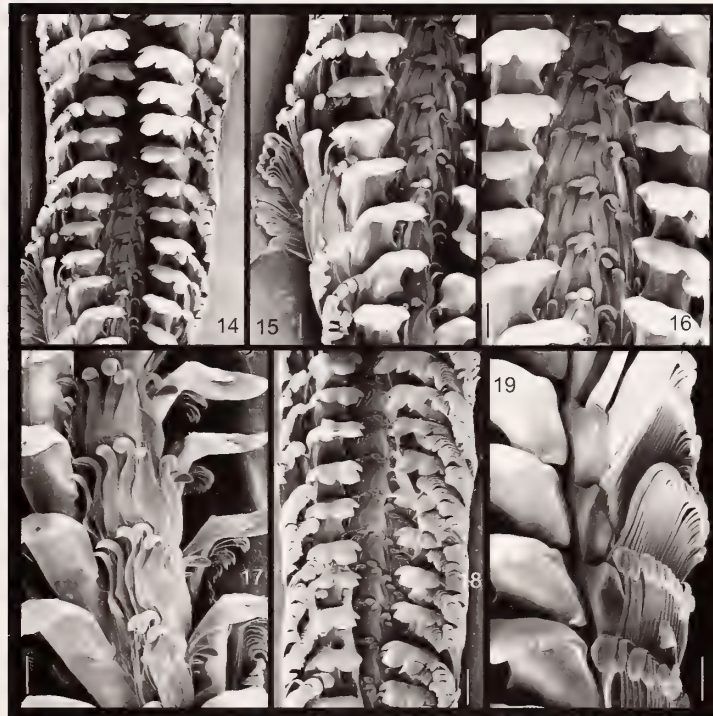
Description: *Shell* (Figures 1–13). Up to 20 mm. Outline elliptical, width about 70% of length (Figures 1, 4, 5, 12, 13). Normally tall, height more than half of length; profiles straight or slightly convex (Figures 2, 3, 10, 11) in both (anterior and posterior) slopes. Color pale brown, greenish beige and white, with many variations and combinations of these colors, normally in radial mosaic of spots (Figures 1–3, 9, 12). Sculpture consisting of about 50 relatively strong radial ribs (Figures 1, 8, 12); each rib normally three times wider than tall, profile quite rounded, separated from neighboring ribs by interval equivalent to about ¼ of rib's width; cords normally stronger in region closer to edges, arranged normally in pattern consisting of stronger cords separated by three slightly narrower rib (Figure 8). Concentric sculpture normally weak, consisting of undulations and small, commarginally aligned nodes of radial ribs (Figures 1, 8, 12). Apical regions normally eroded (Figures 9, 12). Walls thick (Figure 3). Edges thick (as thick as remainder of shell), bearing small irregular projections corresponding to radial sculpture (Figures 4, 5, 13). Foramen central or displaced anteriorly up to 10% of fraction of shell length (Figures 1, 12); occupying about 1/80 of dorsal shell surface area; outline somewhat elliptical (average length/width ratio = 1.45), with irregular, lateral expansions in middle (Figures 6, 7, 13). Inner surface glossy and whitish-green (Figure 13), reddish region close to apex in some specimens (Figures 4). Blue callus surrounding foramen (Figures 4, 7, 13), occupying about 5% of total inner surface, possessing about same thickness as remaining shell wall, differentiated in being glossier and by scale-like edges. Muscle scar very weak, practically imperceptible.

Young forms (Figure 40) showing smooth, symmetrical, almost planispiral protoconch, of one whorl, white; projected posteriorly and ventrally, slightly placed to left. Protoconch width approximately 0.2 mm. Teleoconch with convex anterior and concave posterior slopes. Foramen about three times longer than wide; located between middle and posterior third between anterior edge and protoconch; middle portion with distinct expansions about a third of whole orifice in size. Sculpture similar to that of large shells, except in being more delicate, and by predominance of radial ribs.

Head-foot (Figures 5, 10, 20, 22, 23, 27). Mostly unpigmented, except region of neck, with transverse dark brown spots (Figures 5, 10), sometimes coalescent. Head preceded by long neck of about half of foot in length and 1/3 of foot's width; almost cylindrical; snout continuous with neck in axis and width. Cephalic tentacles located between middle and anterior thirds, on each side; each tentacle tapering gradually, slightly longer than snout; tip pointed. Ommatophores of approximately same width as tentacles' base and about



Figures 1–13. *Fissurella mesoatlantica* shell aspects. Figures 1–8. Holotype (length = 14.0 mm). Figure 1. Dorsal view. Figure 2. Right view. Figure 3. Right-slightly ventral view. Figure 4. Ventral-inner view. Figure 5. Whole specimen, ventral view (fixed). Figure 6. Detail of foramen region, dorsal view. Figure 7. Same, ventral-inner view. Figure 8. Detail of sculpture in left-posterior quadrant. Figure 9. Two *in situ* specimens on calcareous algae (MZSP 86743, each with 15 mm). Figure 10. Paratype MZSP 86743, alive, right-slightly ventral view (length = 15.8 mm). Figures 11–13. Paratype MZSP 86562 (length = 14.6 mm). Figure 11. Whole left view (specimens inside). Figure 12. Dorsal view (specimen inside); 13. Ventral-inner view.

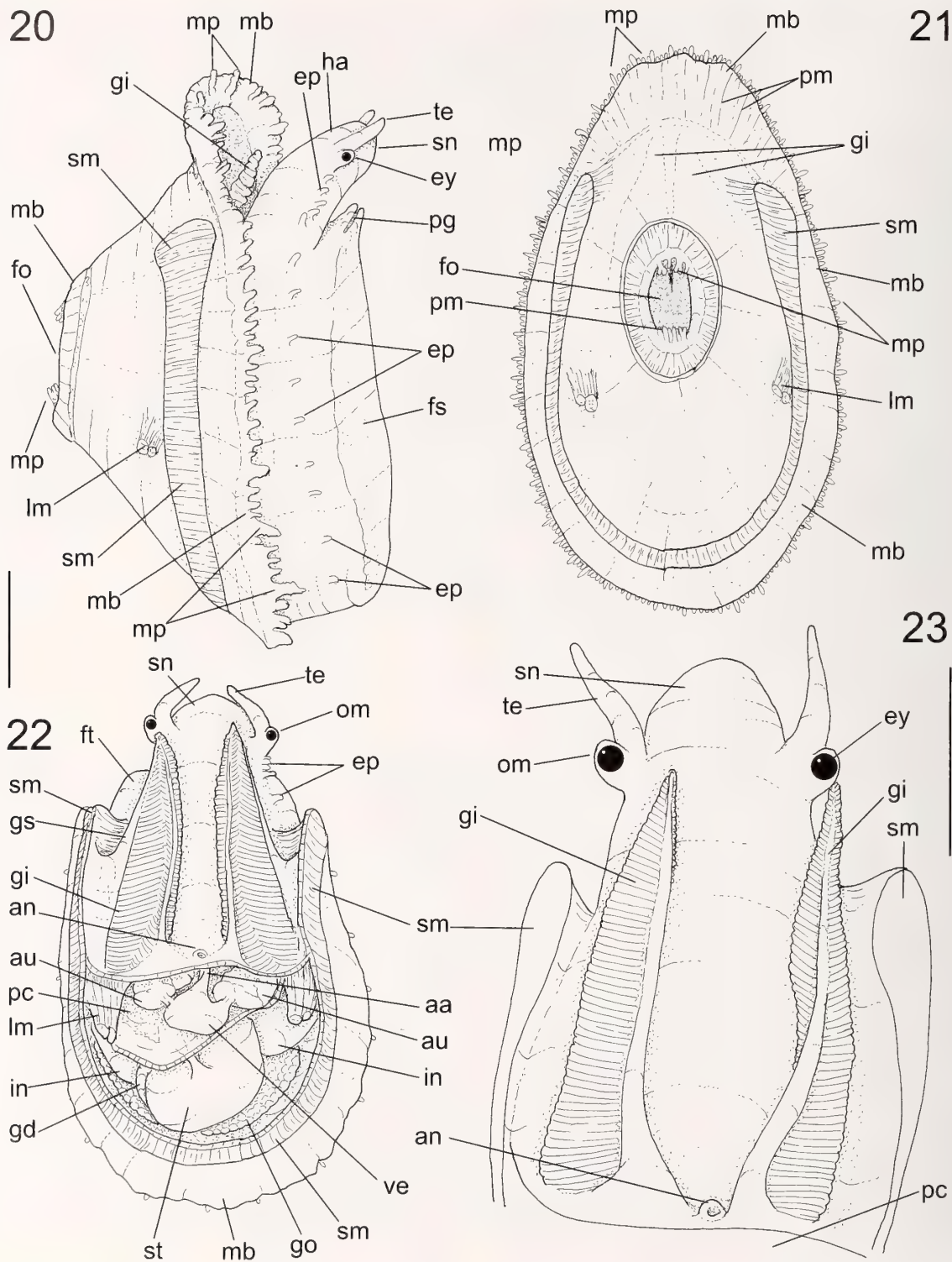


Figures 14–19. *Fissurella mesoatlantica* radulae in SEM. Figures 14–17. Holotype. Figure 14. Whole view in middle region. Figure 15. Detail of marginal area. Figure 16. Detail of central area. Figure 17. Detail of central area in region longitudinally folded; 18–19. Paratype MZSP 86743. Figure 18. Whole view of central region. Figure 19. Detail of marginal area. Scale bars: 14, 18 = 100 μ m; remaining = 50 μ m.

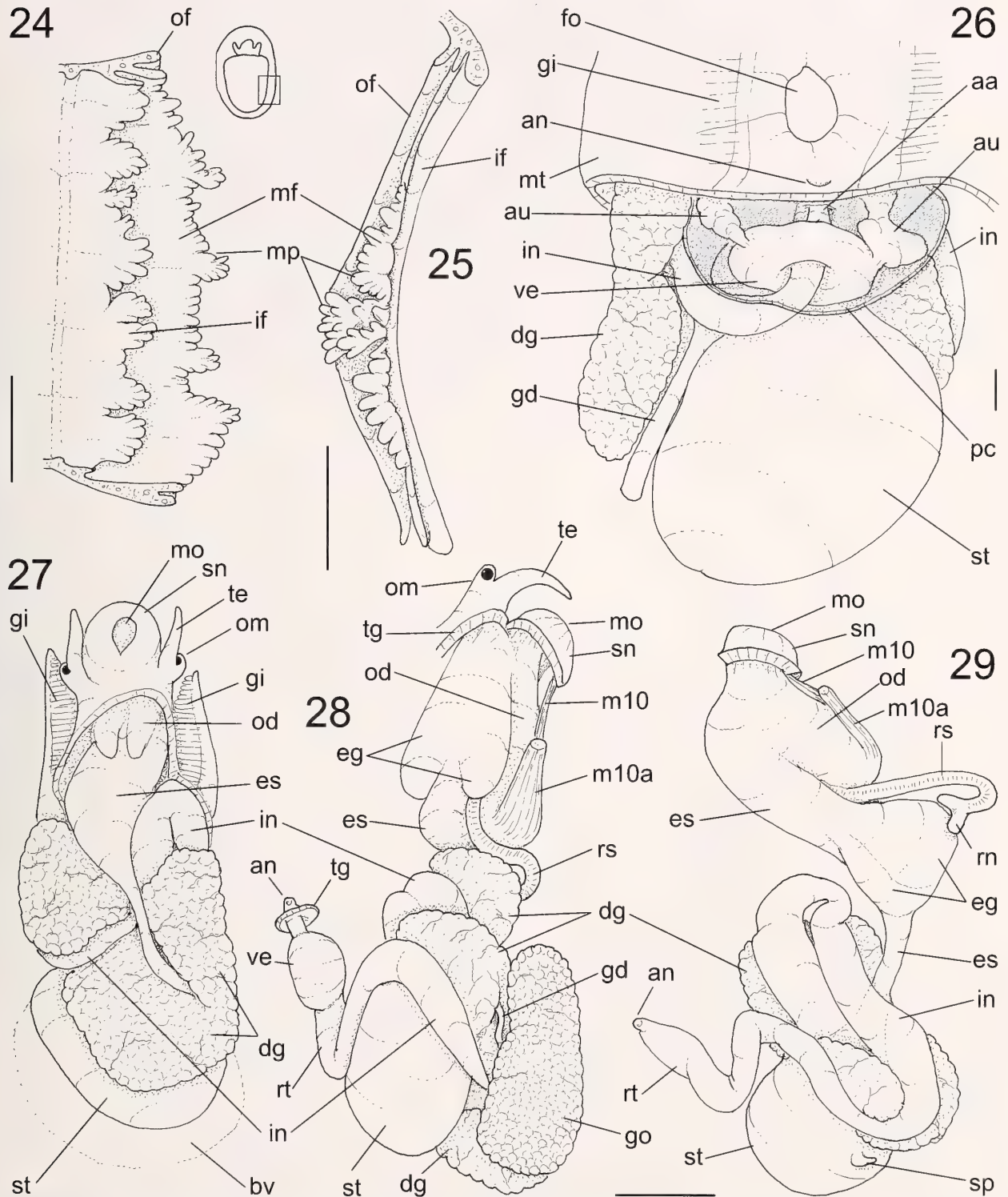
1/4 tentacles' length; located just posterior to tentacles' origin; tip rounded; eye occupying about half of ommatophore volume (Figure 23; ey). Snout almost cylindrical, weakly tapering towards anterior; anterior end rounded; mouth central, occupying about 1/4 of anterior surface. Epipodium marked only by a series of horizontally aligned tentacles (Figure 20; ep), located approximately in middle between sole and mantle edge; each tentacle about four times as tall as wide, length approximately same as ommatophore and about 1/6 its width; five epipodial tentacles aligned on both sides of neck, just posterior to cephalic tentacles, separated from each other by distance equivalent to their width; remaining epipodial tentacles much more widely spaced, interval equivalent to 6–7 times their width; about 10 pairs of tentacles in region dorsal to foot. No differentiated epipodial sensory organ (ESO) detectable. Foot occupying about 80% of shell aperture, edges simple (Figures 5, 10), thick (central region with about 1/5 of shell height). Anterior furrow of pedal gland about 1/3 of foot width. Propodium about 1/10 of foot's length, touching ventral base of neck. Shell muscle symmetrical; posterior region about 1/7 of shell height; gradually becoming broader towards anterior; anterior region weakly curved dorsally, about 1/4 of shell height (Figures 20, 21); origin in shell located

approximately between middle and marginal thirds of shell. Shell muscle protruding inside pallial cavity in anterior region (Figure 22). Pair of longitudinal muscles (Figures 20–22; lm); originating laterally in elliptical area equivalent to 1/100 of inner shell surface, between posterior and middle thirds of shell, just dorsal to adjacent region of shell muscle; running towards anterior; dorsal part inserting in posterior base of gills (Figure 31); ventral part lying along dorsal head integument, splaying along neck base. Haemocoel widely continuous with visceral cavity (Figure 27).

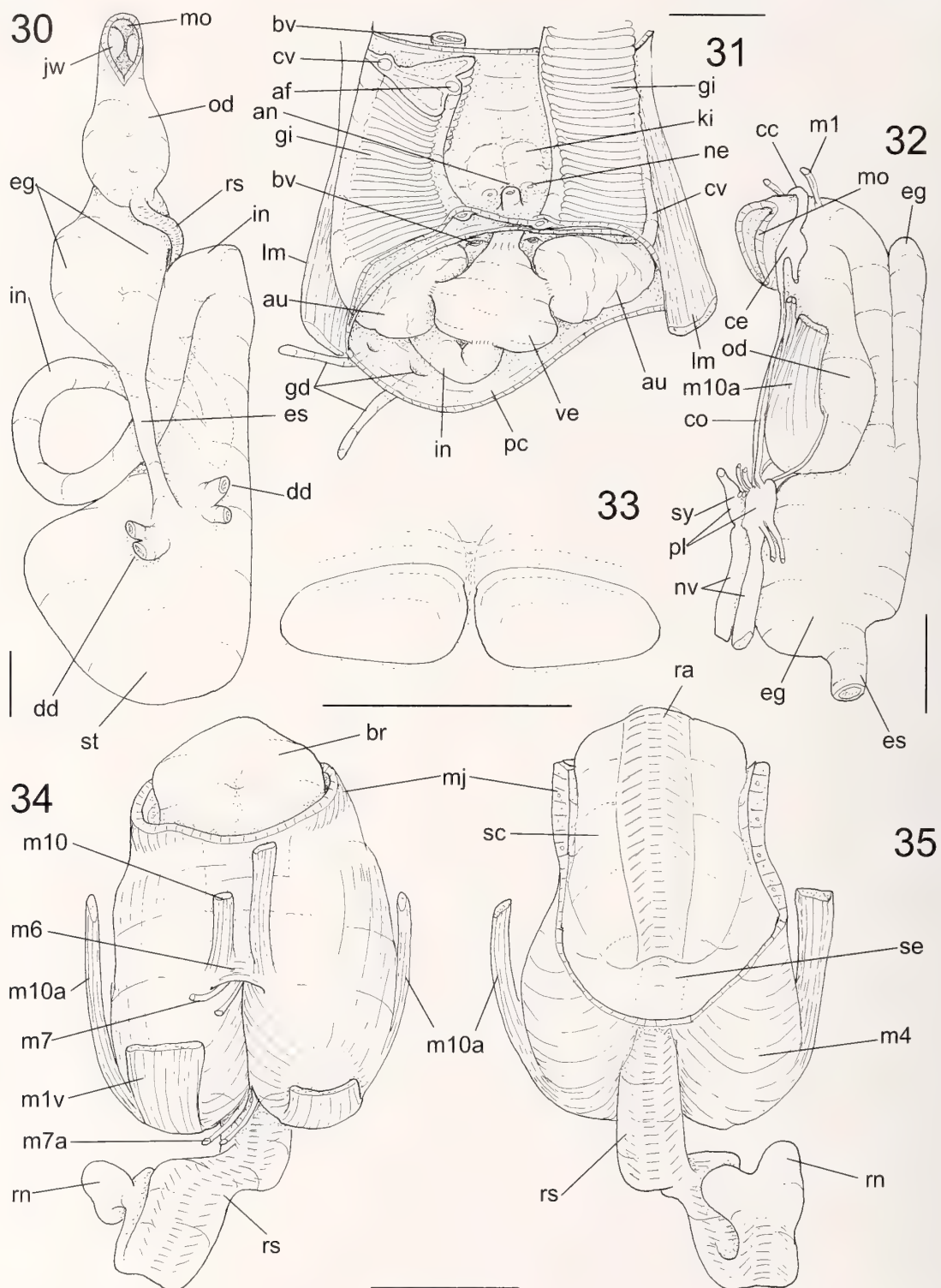
Mantle organs (Figures 22–25, 31). Mantle edge in periphery of shell trifoliate (Figures 10, 20, 21, 24). Outer fold smooth, simple, about 1/3 of shell wall thickness; about twice as long as thick. Middle and inner folds similar in size and organization, length about double of outer folds and with about same thickness; all around papillate, each papilla approximately same length of outer fold, about twice as long as wide; both folds possessing regular projections forming longer, papillate small tentacles projecting beyond shell's edge (Figure 10) a distance equivalent to twice of each fold's height; these small and long tentacles arranged somewhat intercalated, interval equivalent to three times their base (Figure 24). Mantle edge in foramen similarly arranged to shell edge; except for



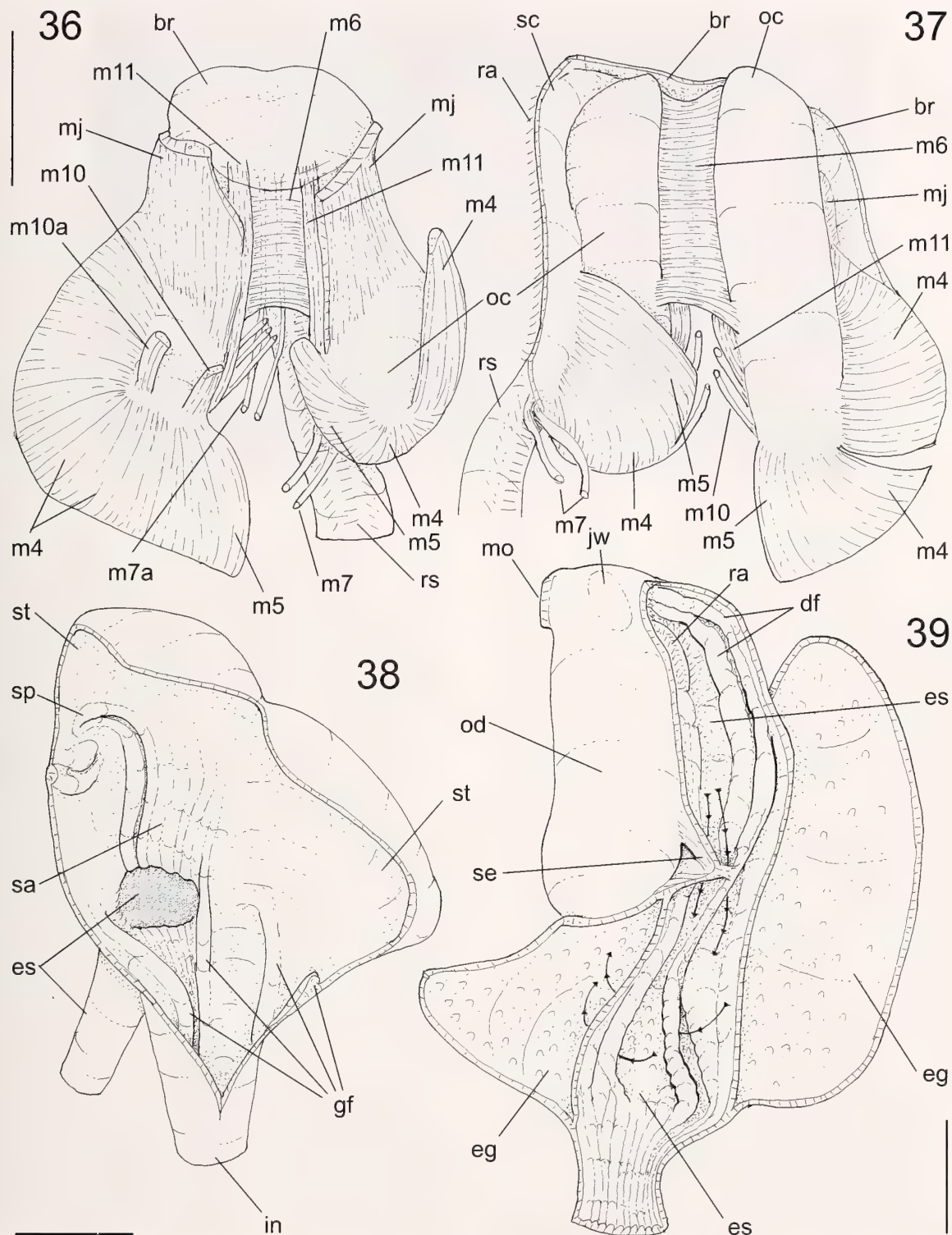
Figures 20–23. *Fissurella mesoatlantica* anatomy. Figure 20. Specimen removed from shell, whole right view, pallial cavity slightly deflected. Figure 21. Same, dorsal view. Figure 22. Same, dorsal region of mantle removed. Figure 23. Detail of head and pallial cavity floor, dorsal view. Scale bars = 2 mm.



Figures 24–29. *Fissurella mesoatlantica* anatomy. Figure 24. Detail of indicated portion of mantle border, inner view. Figure 25. Anterior half of mantle border of foramen, straightened, posterior view. Figure 26. Pericardium and adjacent region of visceral mass and pallial cavity, dorsal view, visceral portion of mantle removed. Figure 27. Haemocoel as *in situ*, ventral view, foot and shell muscle removed, a portion of pallial structures also shown. Figure 28. Same, right view, topology of some adjacent structures also shown. Figure 29. Digestive system as *in situ*, right view. Scale bars = 24–26 = 0.5 mm; 27–29 = 2 mm.



Figures 30–35. *Fissurella mesoatlantica* anatomy. Figure 30. Digestive tubes as *in situ*, ventral view, some portions seen by artificial transparency. Figure 31. Pericardium and adjacent region of pallial cavity, dorsal view, some adjacent visceral and muscular structures also shown, dorsal wall of pericardium removed, adjacent layers of membranes sectioned in order to show main vessels and ducts *in situ*, left gill transversally sectioned to show its constituents. Figure 32. Buccal mass and nerve ring as *in situ*, left view. Figure 33. Jaw plates, inner-ventral view, mouth positioned in inferior side. Figure 34. Odontophore, ventral view. Figure 35. Same, dorsal view. Scale bars = 1 mm.



Figures 36–39. *Fissurella mesoatlantica* anatomy. Figure 36. Odontophore, ventral view, inner layer of structures partially removed, right muscles (left in Figure) deflected, some muscles and radular sac only partially shown. Figure 37. Same, dorsal view, both cartilages deflected, subradular membrane sectioned longitudinally, radular sac and ribbon deflected to left with intrinsic muscles attached to them, right muscles deflected. Figure 38. Stomach, dorsal view, sectioned longitudinally in its intestinal side. Figure 39. Buccal mass and adjacent region of esophagus, left view, esophagus and esophageal gland sectioned longitudinally, inner surfaces exposed, communications among chambers shown by arrows, jaw seen by transparency. Scale bars = 1 mm.

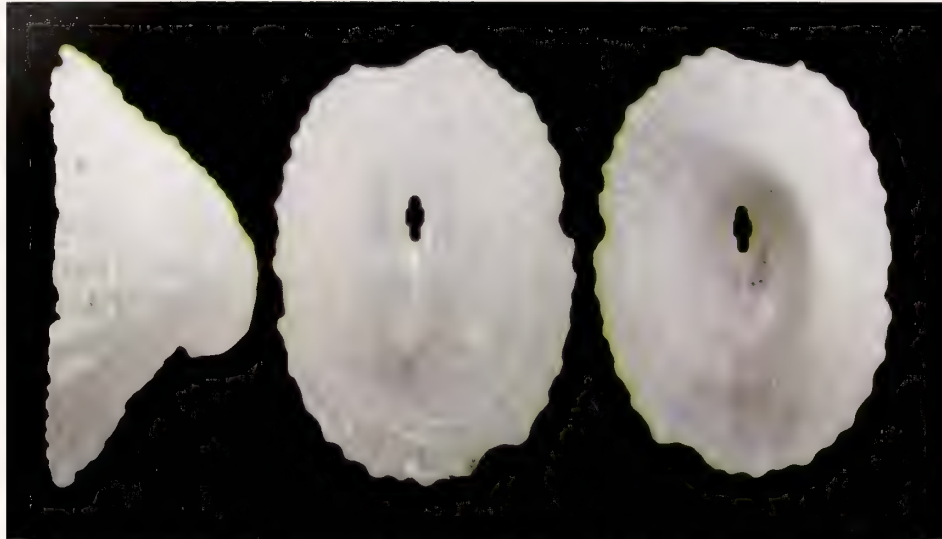


Figure 40. *Fissurella mesoatlantica* shell of young specimen, MZSP 87435; right, dorsal, and ventral views respectively. Length = 2.8 mm.

only middle fold possessing papillae, concentrated in anterior and posterior regions (Figure 21); papillae forming long small tentacles only close to median line, gradually disappearing laterally. Pallial cavity with about half shell's area in depth, symmetrical; its posterior end located just posterior to foramen. Pair of gills symmetrical, each gill about as long as pallial cavity, about 1/4 its width; lateral suspensory stalk (surrounding efferent ctenidial vein) with about half of length attached to shell muscle's dorso-lateral surface (Figures 22, 23, 31); median stalk (surrounding afferent gill vessel) almost completely free, only attached at posterior region close to anus (Figures 22, 26, 31). Gill filaments symmetrical, tip of each leaflet rounded, turned medially (Figure 31). Osphradium inconspicuous. Anus located medially in pallial cavity posterior end (Figures 22, 26, 31). No detectable hypobranchial gland.

Visceral mass (Figures 22, 26–31). Organized as internal mould of shell, more concentrated posteriorly, surrounded ventrally and laterally by shell muscle; continuous with head-foot haemocoel. Volume of visceral sac approximately half of that of shell. Renopericardial area located as most dorsal structure, just posterior to foramen and to pallial cavity; occupying about 1/4 of visceral volume. Stomach occupying central and posterior region, about 1/3 of visceral volume. Digestive gland greenish brown, located in ventral and lateral regions, between stomach and foot, occupying about 1/4 of visceral volume. Gonad white, located mostly in middle of right side; normally about 1/8 of visceral volume. Digestive tubes filling remaining regions of visceral sac, mostly in posterior and dorsal regions (Figures 28, 29). A conspicuous blood sinus

surrounding ventral and posterior regions (Figure 27: bv) of visceral sac floor.

Circulatory and excretory systems (Figures 22, 26, 31). Pair of auricles located laterally, receiving in their antero-lateral corner ctenidial vein from outer edge of gills (Figure 31: cv); volume of each auricle approximately 1/4 of that of pericardium; walls thin, translucent. Ventricle central, surrounding short portion of rectum crossing through pericardium (Figure 28: ve); volume equivalent to that of each auricle; walls thick. Connection between ventricle and auricles simple, on each side of ventricle. Afferent gill vessel (Figure 31: af) originating mostly from haemocoel, running along median side of gills. Renal tissue small, only detectable in pallial cavity roof, in region just anterior to anus (Figure 31: ki); possessing central furrow and a volume equivalent to 1/10 of pericardium. Pair of nephrostomes located on each side of anus, located slightly dorsal and at posterior end of renal tissue. Renal tissue solid, white.

Digestive system (Figures 27–39). Buccal mass about 1/8 of haemocoelic volume, located just posterior to mouth (Figures 27, 28). Odontophore occupying about half of buccal mass ventral volume. Pair of jaw plates (Figure 33) thin, translucent, located in middle of buccal cavity's dorsal wall (Figure 39: jw); each plate trapezoidal, located close to median line, anterior edge slightly thicker than posterior edge. Inner surface of dorsal wall of buccal mass possessing a pair of longitudinal folds (Figure 39: df), each fold's width and height about 1/4 of local width; space between both folds equivalent to 1/4 their width; remaining areas smooth. Odontophore muscles (Figures 34–37): **mlv**, pair of posterior protractor muscle of odontophore

(Figure 34), wide and very thin, originating in ventral region of mouth, running posteriorly bordering ventral surface of odontophore, inserting superficially in odontophore's posterior region over area equivalent to 1/4 of odontophore width; **m4**, main pair of ventral tensor muscles of radula (Figures 36–37), originating from lateral and posterior edges of odontophore cartilages; surrounding dorsal lateral portions of cartilages, wide and thick, inserting at ventral surface of radular sac in its portion crossing odontophore, mainly in its posterior and lateral regions; **m5**, pair of auxiliary ventral tensor muscle of radula, wide and thick, as medial continuation of m4 pair, but located more medially, originating from median and posterior edges of odontophore cartilages (Figures 36, 37), inserting along median line in radular sac portion crossing odontophore (Figure 37); **m6**, horizontal muscle, thin and wide, connecting median edges of both odontophore cartilages from their anterior end, up to level between middle and posterior thirds (Figures 36, 37), anterior region placed slightly towards ventral surface of cartilages, with short posterior portion located on dorsal surface (Figure 37); **m7**, pair of small and narrow dorsal tensor muscles of radula (Figure 36), originating from haemocoel's ventral region at posterior level of odontophore, running dorsally, penetrating medial region of odontophore just anterior to radular sac penetration into odontophore, penetrating radular sac, splaying in this region of ventral side of radular ribbon; **m7a**, pair of small and narrow ventral tensor muscles of radula (Figure 36), originating from and initially running with m7 pair, gradually flanking m6 dorsal surface close to median line, inserting in small region of subradular cartilage's ventral end; **m10**, small pair of ventral protractor muscles of odontophore (Figures 29, 34, 36), originating from ventral region of mouth, running posteriorly bordering ventro-anterior region of odontophore, penetrating through ventral membrane of odontophore just anterior to m7 pair penetration, inserting in median region of odontophore cartilages' ventral and posterior surface (Figure 36); **m10a**, pair of narrow ventro-lateral protractor muscles of odontophore (Figures 32, 34–36), originating from same region of pair m10, but more laterally, running posteriorly flanking ventral and lateral region of odontophore, inserting in same region of m10 pair but more laterally (Figure 36); **m11**, main pair of ventral tensor muscles of radula (Figures 36, 37), originating from median-posterior edge of odontophore's cartilages, running along lateral region of m6's ventral surface, inserting in ventral end of subradular cartilage between middle and lateral halves; **mj**, jaw and thick peri-buccal muscles (Figures 34–37), originating from both odontophore cartilages, in their middle and anterior regions of outer surface (Figure 36), running ventrally, partly through

subradular membrane (Figure 37), surrounding afterwards mouth opening. Odontophore *non*-muscular structures: **oc**, pair of odontophore cartilages, antero-posteriorly elongated, about four times longer than wide, laterally flattened (about half of their width), about as long as odontophore, anterior end blunt, tip dislocated medially, posterior end rounded; **sc**, subradular cartilage in oral cavity occupying most of expose portion of odontophore (Figure 35) in elliptical outline; **br**, subradular membrane, covering entire region of odontophore exposed into oral cavity (Figures 34–36), thin, translucent, surrounding externally jaw and peribuccal muscles (**jw**) (Figure 37).

Radular sac with about twice length of odontophore (Figures 28–30, 34, 35), encased between esophageal gland and adjacent portion of intestine; width about 1/5 of odontophore. Radular nucleus blunt, widely bifid, about 1.5 times radular sad width (Figures 34, 35: **rn**). **Radula** (Figures 14–19): right and left sides asymmetrical, rachidian tooth located at intermediary level between both sides. Rachidian tooth with triangular base, tip blunt, curved posteriorly, base about twice as long as wide (Figures 17, 18); wider portion about 12% of total radular width, length about 20% of radular width; curved tip about 20% of total tooth size. Lateral teeth in six pairs. Four median pairs of lateral tooth similar to rachidian (Figures 16–17), except for narrower base, weakly curved surrounding edge of rachidian's base; this set of four lateral teeth occupying about 20% of radular width in each side. Lateral tooth five, or dominant tooth, much larger, about five times wider and thicker than remaining lateral teeth (Figures 15, 16); base rectangular, with blunt, low cusp in middle region of median edge; tip curved almost perpendicularly, about 20% wider than base, weakly curved inwards, four wide, blunt, terminal cusp occupying about half of tip's width, medial cusps with about 1/5 of terminal cusps' size, both lateral cusps decreasing by a factor of approximate 75% in relation to terminal cusp; lateral tooth five occupying about 15% of radular width. Lateromarginal plate subtriangular (Figure 19); low, lacking projection, cutting edges or cusps, proximal portion narrow, increasing gradually along same distance of any tooth length, producing sinuous distal edges; an oblique, longitudinal thickness ending in base of more distal projection. About 20–22 pairs of marginal teeth, gradually diminishing in size towards periphery (first marginal about twice as large as last one); each one consisting of long rod, with curved distal third (Figures 15, 19); average width of each tooth approximately 5–7% of length; tip pointed, somewhat flat (about 20% wider than proximal rod), each side with 7–8 small, sharp pointed cusps; each cusp about 1/3 of local width of tooth, turned distally, located close to each other, aligned on both sides up to distal end, with a terminal, similar sized cusp; each set

of marginal teeth approximately 9–10% of radular width.

Anterior esophagus with dorsal folds gradually crossing to right side (Figure 39). In this region, ventral fold flanking left side of aperture of esophageal gland; dorsal fold flanking dorsal edge of another aperture to esophageal gland, with its pair (flanking ventral edge of this aperture) as another similar sized fold bordering this aperture; between this fold and ventral fold a wide (about half of local esophageal width), longitudinal furrow, connecting oral cavity directly to posterior esophagus; this wide furrow covered by glandular papillae of same fashion of those of esophageal gland. Esophageal gland with two openings from central region of anterior esophagus described above; remaining a blind-sac of approximately same size as odontophore; originated from right side of esophagus, running initially along ventral region of esophagus, surrounding its left side, located afterwards on dorsal side of esophagus, reaching middle level of buccal mass (Figures 32, 39: eg). Inner surface of esophageal gland completely covered by uniform mosaic of papillae; each papilla white, about as tall as thickness of adjacent wall of esophagus, tip rounded, located very close to each other. Posterior esophagus about as long as anterior esophagus (i.e., its portion through esophageal gland) (Figures 29, 30), with about 1/3 of odontophore's width; inner surface bearing 8–10 longitudinal, low, narrow folds, somewhat uniform in size, located close to each other (Figure 39); these inner folds gradually disappearing posteriorly, producing smooth surface (Figure 38: es). Esophageal insertion in middle region of ventral stomach surface (Figures 27–30), in such two pairs of ducts to digestive gland originates (Figure 30: dd), one pair in each side.

Stomach approximately 1/3 of visceral volume, lying about in its central region (Figures 22, 27–30), wide, antero-posteriorly flattened (about twice wide than tall); wide region posterior, gradually narrowing towards anterior and left (Figure 30), reaching posterior level of buccal mass inside haemocoel (Figures 27, 28). Gastric inner surface mostly smooth (Figure 38); a pair of gastric folds originating in posterior region of esophageal insertion, running posteriorly very close to each other along ventral surface, ending in short curve in small, almost vestigial gastric caecum (Figures 29, 38: sp), located in middle level of gastric ventral-right surface; another pair of similar folds originating in right gastric inner surface with similar characters has these folds, but about 1/4 shorter (Figure 38); special sorting area located to left of these longitudinal folds (Figure 38: sa), possessing 4–5 longitudinal, low folds, somewhat uniform in size, very close to each other, about twice as wide as tall, about 2/3 of each longitudinal folds' width, each fold running from esophageal insertion posterior-left, fading at posterior

level from gastric caecum. Four pairs of longitudinal folds on intestinal side of stomach (Figure 38) situated about equidistantly from each other; two of them originating on each side of esophagus, running along right side, between these two 6–8 longitudinal, low folds, each about 1/3 size of main folds; other two folds located on opposite sides of main folds, except in having smooth region between (Figure 38: gf). Intestine relatively short, its origin in stomach unclear, relatively short – about as long as stomach if straightened; width uniform along its length, about 1/7 of wider region of stomach; running through digestive gland and gonad (Figures 27–30); inner surface mostly smooth and simple. Rectum short, passing through pericardium (Figures 26, 28, 31). Anus a very short papilla located medially at end of pallial cavity (Figures 23, 28, 31: an).

Genital system. Gonad described above (visceral mass). From it two gonoducts running from ventral to dorsal through digestive gland and stomach (Figures 22, 26, 31); each duct narrow; walls translucent, thin; both simply inserting in ventral-left side of pericardium (Figure 31: gd).

Central nervous system (Figure 32). Nerve ring located between buccal mass and adjacent ventral surface of haemocoel. Pair of cerebral ganglia located in both sides of head; each cerebral ganglion elliptical, about 1/4 of mouth size; cerebral commissure about 1/5 of cerebral ganglion width and 5–6 times longer than it. Pairs of pleural and pedal ganglia located posterior to odontophore, very close to each other. Cerebro-pleural and cerebro-pedal connectives very narrow, running parallel to each other a distance equivalent to eight times cerebral ganglion length. Each pedal and pleural ganglia forming single mass, about 1.5 times cerebral ganglion size, located very close from each other, very short commissure. A particularly large pair of nerves, about half of pedal-pleural ganglia diameter, running posteriorly originating from posterior sides of pedal ganglia (Figure 32: nv).

Measurements (length \times width \times height in mm). Holotype $14.0 \times 9.3 \times 6.5$. Paratype MZSP 86743#1: $13.3 \times 9.1 \times 6.6$.

Distribution. Only known to the São Pedro e São Paulo Archipelago.

Habitat. Intertidal rocks and calcareous algae.

Material examined. Types.

DISCUSSION

The described species is considered in the genus *Fissurella* Lamarck, 1799 (type species *Fissurella nimbosa* Linné, 1758 by monotypy) because it fits in the definition of the genus (e.g., Farfante, 1943: 1–2; McLean, 1984), such as sub-central apex, radial sculpture, and foramen bounded inside by a callus which is not truncated or excavated. Possibly, the

species can belong to the subgenus *Cremides* H. & A. Adams, 1854 [type species *Fissurella barbadensis* (Gmelin, 1791)], because of the radiating sculpture and nodes and crenulated margin. However, as the definition of the fissurellid taxa is poor, mainly related to subgenera, a conservative approach is taken here, considering the species in a wider taxon.

Fissurella mesoatlantica can be easily distinguished from similar species by the height of the shell; normally its shells have a height of about half of their length, a character rarely found in the similar species *F. clenchi* Farfante, 1943; *F. rosea* (Gmelin, 1791) and *F. nubecula* (Linné, 1758). In addition to this character, the following comparisons distinguish these species:

Fissurella nubecula, with which *F. mesoatlantica* has been confused previously (Edwards & Lubbock, 1983), occurs in Mediterranean Sea, West Africa and Canaries Islands (Poppe & Goto, 1991; Ardovini & Cossignani, 2004). *Fissurella mesoatlantica* has a more central foramen, while that of *F. nubecula* is normally placed in posterior third. The sculpture of both species is a quite similar, but *F. nubecula* rarely has nodules along radial ribs, a common feature of *F. mesoatlantica*.

Despite *Fissurella rosea* having been reported from the Brazilian coast (e.g., Rios, 1994), it appears to be only a misidentification related to red-pigmented specimens of *F. clenchi* (pers. obs.). The species appears to be restricted to the Caribbean Sea (Farfante, 1943; Jong & Coomans, 1988). *Fissurella mesoatlantica* lacks the characteristic red or rose stain at the inner area surrounding the foramen of *F. rosea*, and the foramen is usually round without lateral projections. The sculpture of *F. mesoatlantica* is also more robust and irregular than that normally seen in *F. rosea*.

Fissurella clenchi is the only species of *Fissurella* occurring along the Brazilian coast and is most similar to *F. mesoatlantica*. In shell characters, they are difficult to distinguish, except by the above mentioned taller shell of *F. mesoatlantica*. Also, *F. mesoatlantica* normally has fewer radial ribs (about 50 versus about 70 of *F. clenchi*), the shell outline is normally more rounded (length to width ratio of *F. mesoatlantica* is on average 1.4; in *F. clenchi* about 1.7), and its base is normally arched (Figures 2, 11). In addition to the distinguishing shell characters of these two species with disjunct distribution, some additional anatomical features can be enumerated. *Fissurella mesoatlantica* has simpler papillae at the mantle's border (*F. clenchi* has mostly ramified papillae); the papillae in the foramen are generally restricted to the anterior and posterior margins in *F. mesoatlantica* (Figures 21, 25), while they are more uniformly distributed in *F. clenchi*. The epipodial tentacles of *F. mesoatlantica* are more separated from each other and fewer in number compared to *F. clenchi*, which has about 10–12 closely spaced pairs near the head (while *F. mesoatlantica* has

five pairs). The anus is papilla-like in *F. mesoatlantica*, but is sessile in *F. clenchi*.

Fissurella emmanuella Métivier, 1970 (Leal, 1991; Rios, 1994) is an endemic species from Fernando de Noronha archipelago, Brazil, the closest to ASPSP. *Fissurella mesoatlantica* can be easily distinguished by lacking the characteristic brown pigment of the outer surface of the shell, and the green color of the inner shell's surface; additionally, *F. mesoatlantica* has a much more developed sculpture. However, both species have normally a similar height of the shell. Both species are also representative of the tendency for endemism of the genus *Fissurella* on oceanic islands.

From the remaining species occurring in the north Atlantic (Farfante, 1943), *Fissurella mesoatlantica* also differs: from *F. nimbosea* (Linné, 1758), *F. barbadensis* (Gmelin, 1789), *F. angusta* Gmelin, 1789 and *F. nodosa* (Born, 1780) in lacking such raised radial sculpture; from *F. barbouri* Farfante, 1943, in having a much smaller foramen; and from *F. punctata* Fischer, 1857 and *F. fascicularis* Lamarck, 1822 in having an elliptical outline and a sub-central foramen. Based on relative small size and richness of shell sculpture, *F. mesoatlantica* can not be confused with any species from South Atlantic and Pacific coast of South America (McLean, 1984).

It is important to emphasize that the systematics of the genus *Fissurella* is particularly difficult because of the high variability of their shells, which are moldable to the substrate and are, apparently, influenced by other biotic and abiotic features. The anatomy is apparently more conservative and a more stable source for comparative analysis (pers. obs.). Previously, the anatomy of the fissurellids is poorly known, and the knowledge was restricted to a few species (see references below). *Fissurella mesoatlantica* has the normal anatomy of the family, an enigmatic set of plesiomorphic and apomorphic characters in relation to Gastropoda. Among the plesiomorphic states are the pair of symmetrical gills and auricles and the lack of copulatory organs (Lindberg & Ponder, 2001). Of apomorphic states, the more important are the foramen of the shell, separating in two the mantle border (one surrounding the shell and another the foramen); the single pair of odontophore cartilages (Figure 37) (normally the vetigastropods bear a pair of posterior odontophoral cartilages); the shortness of the gastric caecum and of the intestine (Figure 30) (usually very long in vetigastropods) (Ward, 1966); the pair of well-formed gonoducts connecting the gonad with the pericardium (Figure 31) (normally the gonad attaches directly to pericardium); and the fusion of the pair of pleural ganglia with pair of pedal ganglia (Figure 32). The level of these main modifications, whether an autapomorphy of *F. mesoatlantica* or of another higher taxon (*Fissurella*, Fissurellinae, Fissurellidae),

is still unclear. At least some of them are present in most foramen-bearing fissurellids (Boutan, 1886; Ziegenhorn & Thiem, 1925; Trigo, 1930; Odhner, 1932; Fretter & Graham, 1962; Hickman, 1998; Sasaki, 1998). The size of the mantle's edge and complexity of appendages and papillae is much more modest in *Fissurella* than, for example, in *Diodora* Gray, 1821 and *Lucapina* Sowerby, 1835 (Illigworth, 1902; Stasek & McWilliams, 1973). Although differing in some details, the organization of the genital system of *F. mesoatlantica*, with the kidney as part discharge pathway of the gametes, is typical for the family (Bretos et al., 1983; Beninger et al., 2001; Collado & Brown, 2007).

There is apparently a correlation between tallness of shell in limpets and energy of environmental water (waves or flow) (Vermeij, 1974, 2004): the higher the energy, the higher the shell. In *Fissurella mesoatlantica*, the shell is tall in the high energy environment where it was collected. Waves precluded the collection of this species while submerged; the specimens are only collected during very low tide.

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The Gastropod *Spiricella* (Opisthobranchia: Umbraculidae) in the Recent Caribbean: A truly unexpected finding!

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Abstract. The first record of the genus *Spiricella* Rang & Des Moulins, 1828 is given for the Recent western Atlantic. Until now considered a monospecific genus, the *Spiricella* specimens from Abaco Island, Bahamas, Caribbean, are consistently different from the Recent and fossil shells from the Northeastern Atlantic and West Africa. Despite the paucity of morphological shell features typical for the genus, we consider these Caribbean shells a distinct specific taxon; *Spiricella redferni* n. sp. The genus continues as elusive as ever, and despite this exciting new record and the great extension in geographical range for the genus, we still know nothing of the animal to which these shells belong, nor its ecology.

Key Words: Gastropoda, Opisthobranchia, Umbraculidae, *Spiricella*, new taxon, Recent, Caribbean, Bahamas.

INTRODUCTION

For the second time in two years we are writing about a shell of which little is known. Silva & Landau (2007) discussed the occurrence of *Spiricella unguiculus* Rang & Des Moulins, 1828 in the Pliocene of Portugal, and went on to discuss the Cenozoic palaeobiogeographic distribution of this monotypic genus.

Until now it had been assumed that the genus was restricted to the Northeastern Atlantic and Mediterranean coasts. Much to our surprise two specimens have turned up from the Bahamas (Caribbean) found in shell grit collected at Sandy Point on Great Abaco Island (Figure 1) over thirty years ago by Mr. Colin Redfern. The delay in recognizing these unusual specimens was undoubtedly due to all the literature previous to Silva & Landau (2007) being published in European journals, and highlights the importance of disseminating scientific information.

Systematics

Subclass Opisthobranchia Milne-Edwards, 1848

Order Notaspidea P. Fischer, 1883

Superfamily Umbraculoidea Dall, 1889

Family Umbraculidae Dall, 1889

Genus *Spiricella* Rang & Des Moulins, 1828

Spiricella redferni n. sp.

Figures 2–9

Dimensions and material: Holotype; Figures 2–6, UF422928 (Florida Museum of Natural History, University of Florida), length, 4.25 mm (*ex.* Colin Redfern coll., # 4760).

Other material: Paratype 1; Figures 7–9, UF422929, length, 4.25 mm (*ex.* Colin Redfern coll., # 1704).

Etymology: Named for Mr. Colin Redfern, who found and recognized the shell as new.

Type locality: Collected from beach drift from a beach near the airstrip at Sandy Point on Great Abaco Island, Bahamas (N26 00.00, W77 24.28) (Figure 1).

Type age: Recent.

Description: Shell small, 4.25 mm long, 2.0 mm width, thin, fragile, unguiform, subrectangular, antero-posteriorly elongate, with parallel sides and rounded extremities, convex profile on the dorsal side. Apex strongly eccentric, placed close to the posterior edge and far to the left. Protoconch small, paucispiral, naticiform, sinistrally coiled, consisting of 1.75 smooth whorls, diameter approximately 250 μ m, with a medium-sized nucleus, diameter approximately 90 μ m. The protoconch is partially embedded within the surface of the shell. Transition to teleoconch sharply delimited. Sculpture of the teleoconch absent, except for concentric growth lines, more strongly developed on the

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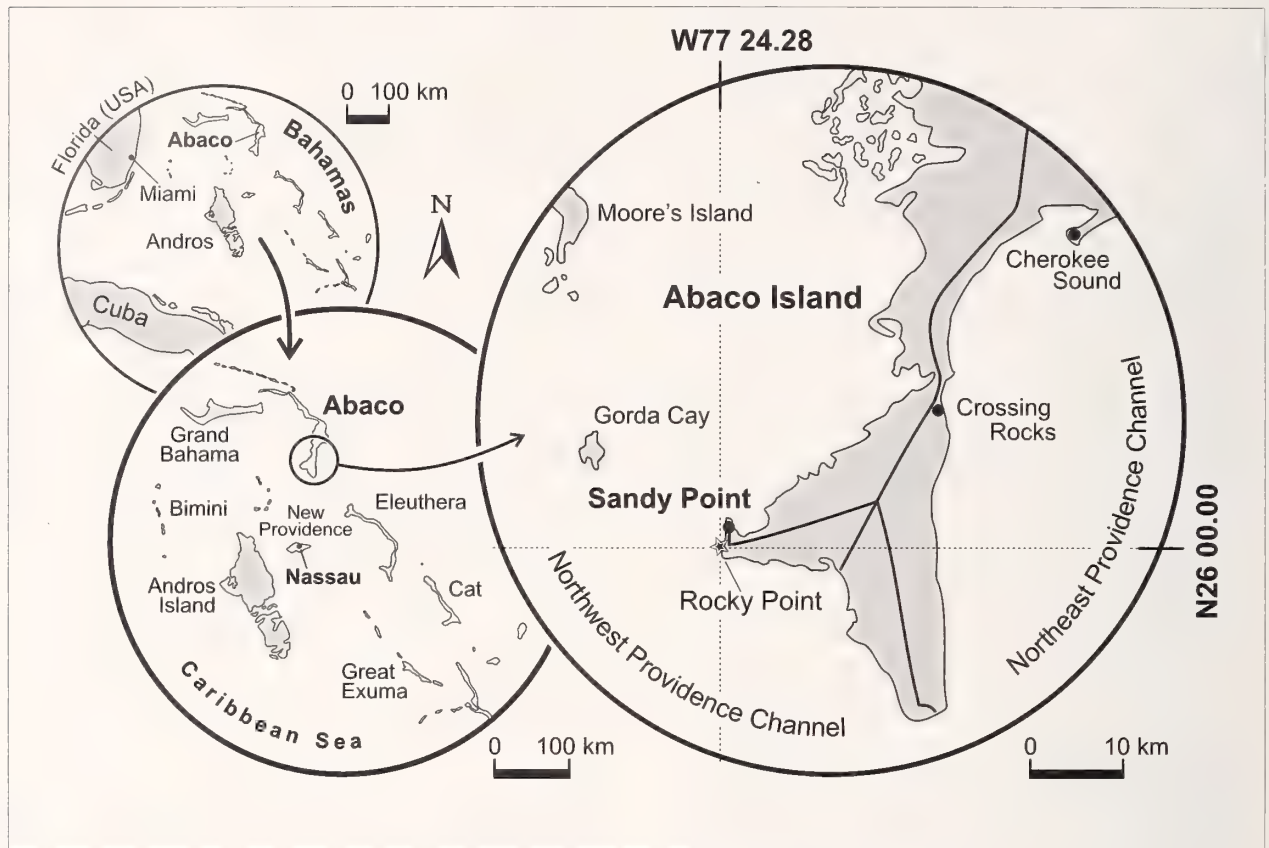
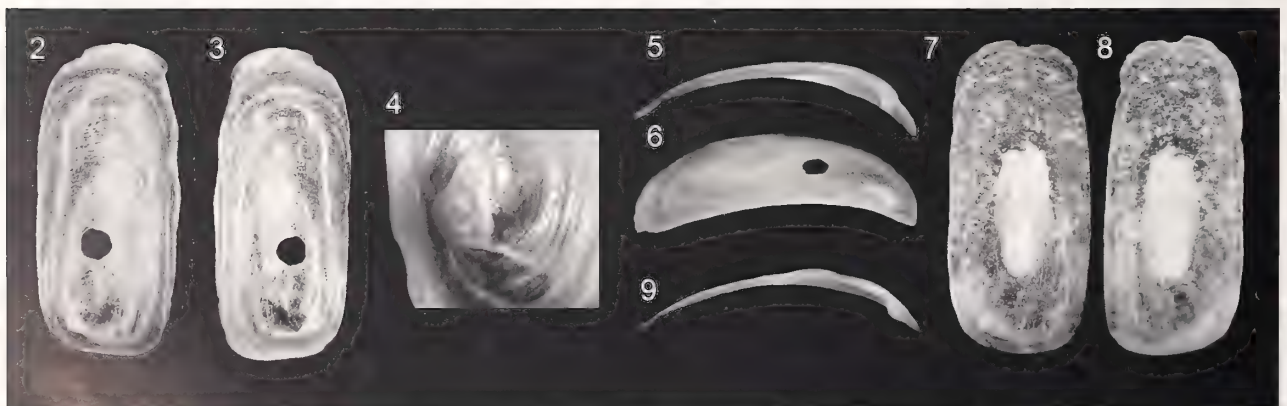


Figure 1. Map showing type locality of *Spiricella redferni* n. sp.

anterior part of the dorsum, giving it a finely rugose appearance. Edge sharp. Ventrums smooth and shiny, with a rounded, thickened rim of variable width (about 0.2–0.25 of the shell width), which is almost absent along the anterior extremity. The apex is represented on the inner aspect by a rounded ridge.

Remarks: Traditionally the genus *Spiricella* has been regarded as monospecific and placed in the Umbraculidae (Janssen, 1984; Hoeksema & Janssen, 1984; Carrozza & Rochini, 1987; Valdés & Lozouet, 2000; Silva & Landau, 2007). Until now all the *Spiricella* specimens, fossil and Recent, had been found in



Figures 2–6. *Spiricella redferni* n. sp. Holotype; UF422928. Collected from beach drift from a beach near the airstrip at Sandy Point on Great Abaco Island, Bahamas. Length, 4.25 mm.

Figures 7–9. *Spiricella redferni* n. sp. Paratype; UF422929. Collected from beach drift from a beach near the airstrip at Sandy Point on Great Abaco Island, Bahamas. Length, 4.25 mm.

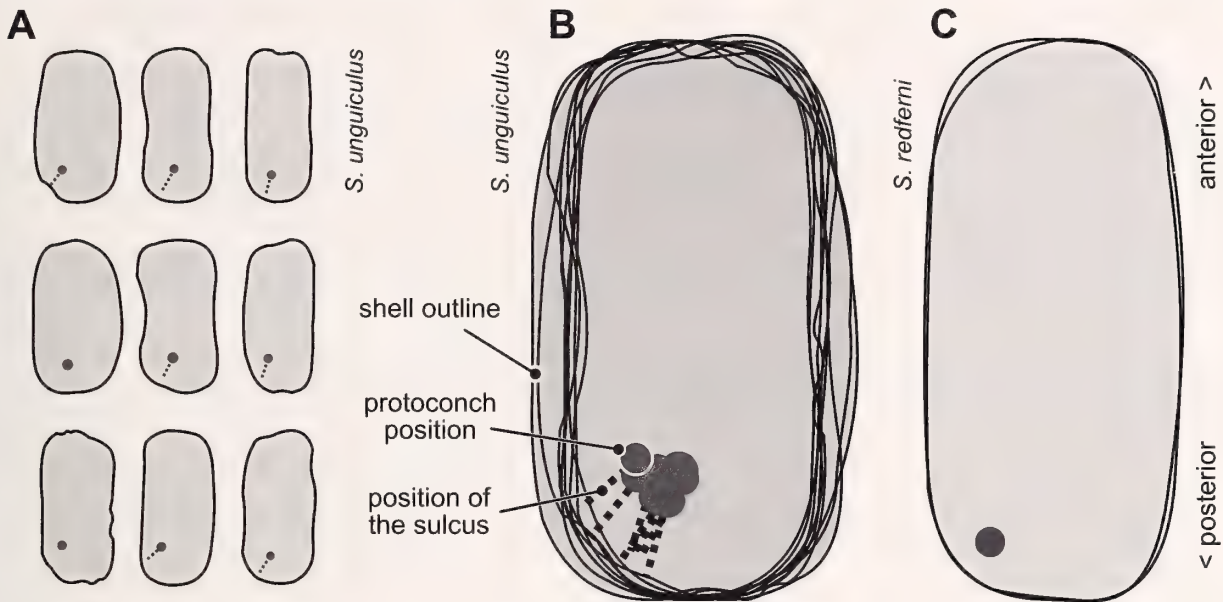


Figure 10. Position of apex in *Spiricella unguiculus* Rang & Des Moulins, 1828 vs. *Spiricella redferni* n. sp.

European Cenozoic basins and in the Northeastern Atlantic and Mediterranean (Silva & Landau, 2007, with references). Still nothing is known of the ecology of this genus, and no living animal or soft parts have ever been found. Unfortunately, these new finds add no new information concerning the ecology of *Spiricella*, as the shells were found in samples of beach drift from the extreme southwest tip of Abaco, between the locality of Sandy Point and the promontory of Rocky Point. Rocks border the beach, with *Thalassia* meadows beyond the rocks. This shell grit contains an assemblage of shells from all the neighboring environments: rocky and sandy substrates, *Thalassia* meadows, as well as deeper water environments, which lie close by.

As pointed out by Silva & Landau (2007), and almost every other researcher struggling to make sense of this genus, problems are posed by the paucity of specimens; fossil and Recent, lack of knowledge of the soft parts, and lack of distinctive shell characters. The eastern shells are fairly uniform in shape, all more or less rectangular, with length/width ratio of 2–2.22. Only the presumably immature Recent shell from Serini, Mauritania is less elongated, with a ratio of 1.79 (Geuze & Hoeksema, 1994). All the shells have a smooth paucispiral protoconch of 1.25–1.75 whorls. The position of the apex is eccentric in all, placed about 1/5 distance from the posterior edge and to the left (Figure 10).

The Bahamian shells are almost identical to the Northeastern Atlantic and Mediterranean ones in overall shape, arched in profile and with similar concentric growth lines. The protoconch is also paucispiral, consisting of 1.75 smooth whorls, but somewhat smaller in total diameter than the eastern

shells (250 μm vs. approximately 330 μm , Valdéz & Lozouet, 2000; Silva & Landau, 2007). The most striking difference between the Bahamian and the eastern specimens lies in the position of the apex. In the Bahamian specimens the apex lies considerably more marginally; more posterior and further to the left than in the eastern shells. An important morphological feature of the eastern shells is a narrow rectilinear sulcus running obliquely from the apex to the edge, absent in the Bahamian shells.

Discussion: The presence of these *Spiricella* shells in the Bahamas posed the question of whether one or two Recent species exist.

From a morphological point of view, despite the lack of characters, there are two consistent differences between the eastern and western shells: the position of the apex and the presence or absence of the sulcus. Although the eastern specimens show some variability in the position of the apex, none comes close to that seen in the Bahamian shells (Figure 10). All the Northeastern Atlantic and Mediterranean shells show a more or less well developed sulcus associated with the apex, which is absent in the two Bahamian specimens. Apart from the differences outlined above, the overall diameter of the protoconch of the Bahamian shells is smaller than that of the eastern specimens. We therefore consider the Caribbean shells to represent a second species of *Spiricella*, *S. redferni* n. sp.

We are not aware of any other fossil or Recent record for the genus in the Americas, or anywhere else outside Western Europe, the Mediterranean and Northwestern Africa. The European literature for the

genus, however, extends back to the Lower Oligocene, Rupelian Stage, of France (Valdéz & Lozouet, 2000). The fossil record would therefore suggest that *Spiricella* originated in the Eastern Atlantic and dispersed westwards. Interestingly, Vermeij & Rosenberg (1993) noted that many of the taxa in their list of westward-dispersing species had no fossil record in the Western Atlantic and appeared to be relatively recent immigrants to the American coasts, but unlike many other westward invaders *Spiricella* apparently has not achieved a wide distribution in the Americas.

Acknowledgments. We would like to thank Mr. Colin Redfern for bringing these interesting specimens to our notice, and donating the type material.

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Functional Anatomy of *Bankia fimbriatula* Moll & Roch, 1931 (Bivalvia: Teredinidae)

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Abstract. *Bankia fimbriatula* Moll & Roch, 1931, is a highly specialized bivalve adapted for boring into wood. Specimens were collected alive from a mangrove region at Praia Dura, Ubatuba, São Paulo, Brazil and maintained in an aquarium at room temperature (21°C) at the laboratory of the Department of Zoology, University of São Paulo. Studies of the anatomy were carried out on both relaxed and preserved specimens. Special attention was paid to the siphons, pallets, ctenidia, labial palps and mantle. The siphons are fairly long, and separated. The inhalant and exhalant siphons have ciliary activity at the tentacles, as described previously for *Nausitora fusticula* (Jeffreys, 1860). The posterior ctenidia are homorhabdic. Each ctenidium of *B. fimbriatula* is formed by the external demibranch only, with the blades in a “V” form. The ctenidia, associated with the rejection tracts of the mantle, present a good mechanism to deal with large quantities of particles, probably an adaptation for life in turbid waters. The labial palps are extremely reduced. The functional anatomy of *B. fimbriatula* suggests that both plankton and wood probably are important as food for this species.

INTRODUCTION

The anatomy of species of Teredinidae has been studied by several authors, including Quatrefages (1849), Menegaux (1889), Ridewood (1903), Sigerfoos (1908), Potts (1923), Lazier (1924), Atkins (1937), Purchon (1939, 1941, 1960), Nair (1957), Bade et al. (1961, 1964a, 1964b), Turner (1966), Rancurel (1971), Saraswathy & Nair (1971), Lopes & Narchi (1998) and Lopes et al. (1998). Some references [Atkins (1937), Purchon (1941, 1960), Clapp (1951), Morton (1970, 1978), Martinez (1987), Lopes & Narchi (1998) and Lopes et al. (1998), are restricted mainly to the structure and function of specific organs.

The functional anatomy of *Bankia fimbriatula* Moll & Roch, 1931, is the main focus of this work; we analyzed the functioning of the siphons, the muscles associated with the siphons and pallets, and the ciliary currents related to the selection of food and particles for elimination. A detailed study of the anatomy and function of the stomach will be presented in a separate paper.

Bankia fimbriatula occurs mainly in tropical warm waters around the world (Turner, 1966). On the Brazilian coast it has been reported from the littoral zone of São Paulo State (Lopes & Narchi, 1998), Paraná State (Müller & Lana, 1986, 1987; Skinner et al., 1993) and Rio de Janeiro State (Silva et al., 1989; Junqueira et al., 1989; Martins-Silva et al., 1990 and Junqueira & Silva, 1991).

The genus *Bankia* Gray, 1842, includes twenty-three species (Turner, 1971) in the subfamily Bankiinae Turner, 1966, thirteen of which occur in the Brazilian littoral.

Among species of *Bankia*, Sigerfoos (1908) studied the anatomy of *Xylotrya gouldi* [= *Bankia gouldi* (Bartsch, 1908)], Clapp (1951) made observations on living Teredinidae and described the siphons of *B. gouldi*. Bade et al. (1961) illustrated and described the mantle of *Bankia minima* [= *Bankia carinata* (Gray, 1827); Turner (1966, 1971)]. Bade et al. (1964a, 1964b) studied the digestive and respiratory systems of the same species. Turner (1966) described the posterior region of *B. gouldi*, and described the anatomy of *Bankia setacea* (Tryon, 1863), *B. campanellata* Roch & Moll, 1931, and *B. australis* (Calman, 1920). Saraswathy & Nair (1971) described the anatomy of *B. indica*. Tan et al. (1993) made a study of the shell and pallets of the early developmental stages of *B. gouldi*.

This paper presents the first anatomical study of *Bankia fimbriatula*.

MATERIAL AND METHODS

Specimens of *B. fimbriatula* were collected during 1992 and 1994 in mangrove trees at Praia Dura, Ubatuba, São Paulo, Brazil (45°15'W, 23°30'S) (Figure 1). This is the second most abundant species of Teredinidae in the area, living at a salinity range from 0–33‰ (Lopes & Narchi, 1993). The animals were kept inside the wood, in a seawater aquarium with constant aeration and at a salinity of 20‰ and a room temperature of 22°C, where

[†] Dr Walter Narchi (died in 2004)

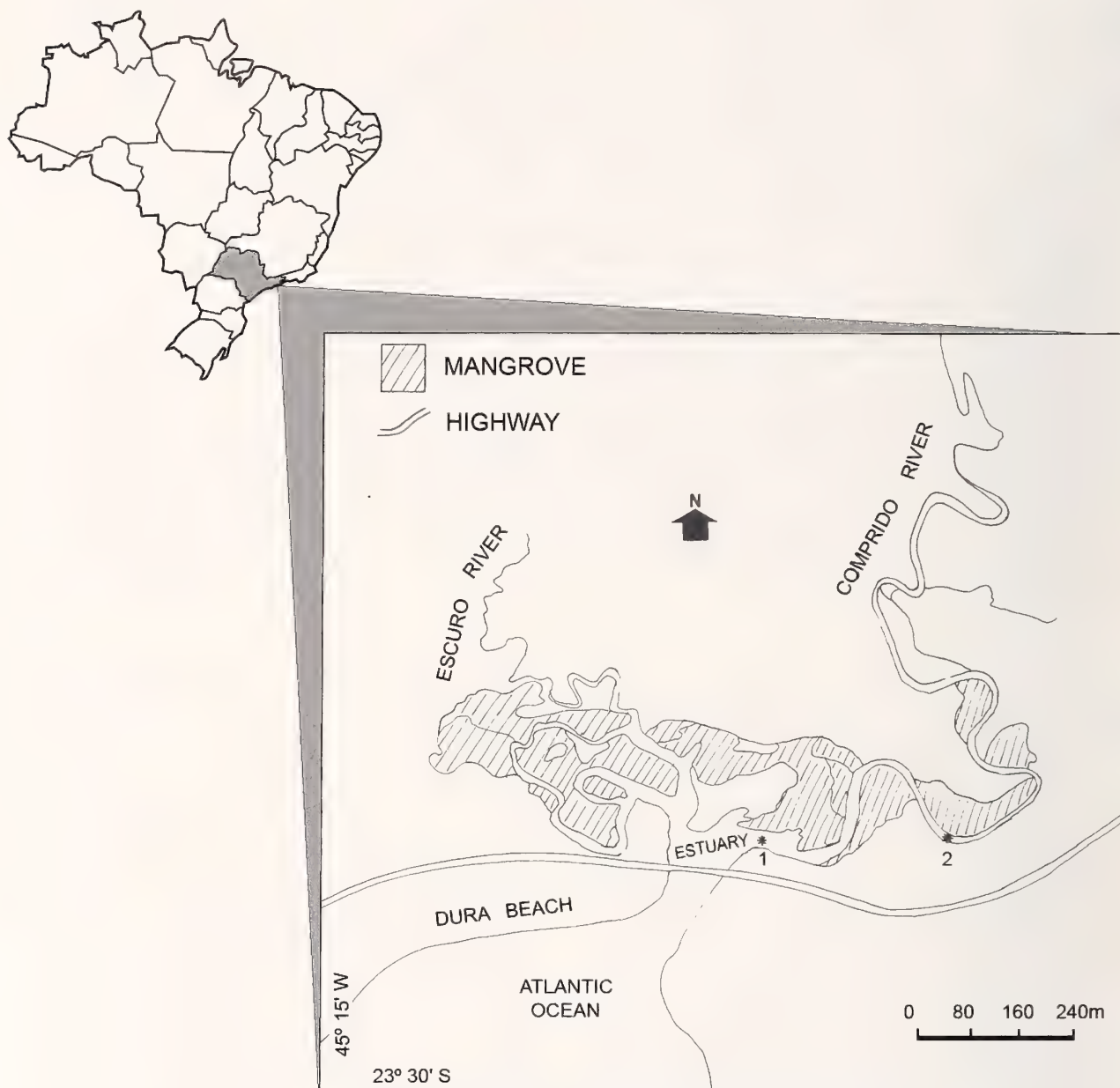


Figure 1. Map of the mangrove region at Praia Dura, Ubatuba, São Paulo, Brazil, with indications of the collection stations (*1 and 2).

they stayed in good condition for almost two years. The study of the functional anatomy was conducted at the University of Brasília where the animals were kept alive in an aquarium with artificial seawater.

Around 50 living and preserved specimens of all sizes were analyzed. Identification of the material was based on Clench & Turner (1946) and Turner (1966, 1971). Identification was confirmed by the late Dr. Ruth D. Turner, Harvard University, USA. A lot of 15 complete specimens (shell, pallets and soft parts)

were deposited in the Museu de Zoologia, Universidade de São Paulo (MZ USP) under the registration number 32061.

Ciliary currents were studied by the application of a suspension of Carborundum (F3), carmine and Aquadag solutions. To help the observation of the different organs, whole animals were stained with Paracarmin and later cleared (Bücherl, 1943).

Some of the anatomical details analyzed were also obtained by transverse sections 6–8 μm thick, of

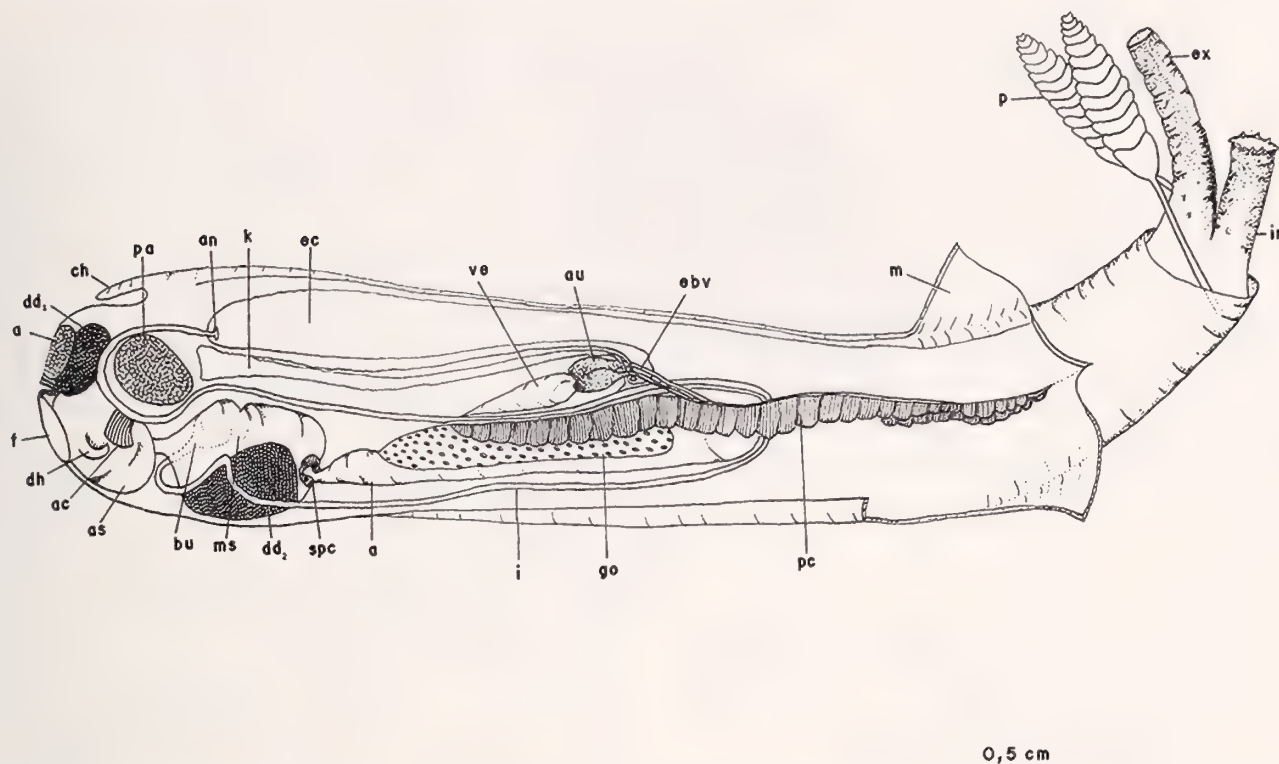


Figure 2. *Bankia fimbriatula*. General topography of the organs after removal of the valve and the mantle from the left side of the body. Abbreviations: a, appendix; aa, anterior adductor muscle; ac, anterior ctenidium; an, anus; as, anterior stomach; au, auricle; bu, bulblike swelling; ch, cephalic hood; dh, dorsal hood; dd₁, dd₂, digestive diverticles; ec, epibranchial cavity; ebv, efferent branchial duct; ex, exhalant siphon; f, foot; go, gonad; i, intestine; in, inhalant siphon; k, kidney; m, mantle; ms, median stomach; pa, posterior adductor muscle; pc, posterior ctenidium; spc, semi-spiral conical projection; vc, ventricle.

animals fixed in Bouin's fluid and stained with Mallory's Triple Stain or Ehrlich's haematoxylin and eosin, according to the method described by Pantin (1948).

RESULTS

General disposition of organs in the mantle cavity

The disposition of the major organs in the mantle cavity of *B. fimbriatula* is shown in Figure 2.

The visceral mass occupies about 60% of the body length and the posterior ctenidia and siphons occupy the remainder.

The stomach has two regions; the appendix or wood-storing caecum is well developed and in the live animal is easily distinguished from the other structures because of its reddish color due to particles inside it.

The digestive diverticula are of two types as defined by Potts (1923) and Morton (1970) for *Teredo navalis* (Linnaeus, 1758): the normal type and the specialized type. In live specimens of *B. fimbriatula* there is no difference between the digestive diverticula in contrast to what Lopes & Narchi (1998) described for *Nausitora*

fusticula (Jeffreys, 1860). In *B. fimbriatula* the differences are only distinct in histological sections.

Males and females have milky white gonads, situated at the region immediately posterior to the distal part of the digestive diverticula.

Contrary to what Turner (1966) states for *B. gouldi*, *B. setacea*, *B. campanellata* and *B. australis*, the heart of *B. fimbriatula* has two intensely dark brown pigmented atria. The ventricle is whitish in color and from it arises a well-developed aorta located on the dorsal surface of the gonads.

The kidney is dorsal to the aorta, extending from the posterior part of the posterior adductor muscle to the distal extremity of the pericardial cavity. The nephrostome opens into the interior of the pericardial cavity and the nephridiopores into the epibranchial cavity, both at the same level of the body. The afferent excretory duct shows, just behind the nephrostome, a globular dilatation whose internal wall is deeply folded and ciliated. The two nephridiopores are placed near each other, being smaller than, and situated posteriorly to, the gonopores.

The anal canal lies in the dorsal region of the visceral mass and extends from the anus to the posterior end of

the gonads, connecting to the epibranchial cavity through a narrow opening.

Shell

The descriptive terminology of the shell is based on Turner (1966). Less than half the external surface of the shell of *B. fimbriatula* (Figure 3) is occupied by the anterior slope. The dorsal region possesses denticulate ridges that are eroded by friction against wood; laterally these ridges are more developed. The umbonal-ventral sulcus is narrow and flat. The dorsal and ventral condyles are obvious, but the umbonal-ventral ridge is poorly defined. The apophysis is flat when viewed transversely, with a sharp extremity near the ventral condyle. The posterior adductor muscle scar is only weakly evident.

Pallets

The pallets of *B. fimbriatula* (Figure 4) possess a long stalk, of the same length as or shorter than the blade. The pallets are elongate and the blades are composed of numerous cone-like elements on a central stalk; these elements are separated and easily removed from the stalk, particularly in dried specimens. The cones have a calcareous base covered with periostracum, which extends as a border. The width and the ornamentation of the periostracal border vary greatly; the border may be smooth, coarsely to finely serrate, or produced laterally as awns.

Variations in the form of the blade could not be related to the age of the animals or to environmental conditions. As all specimens came from the same population and similar ecological conditions this can be interpreted as individual variation, as Lopes & Narchi (1998) observed for *Nausitora fusticula*.

Siphons

As described for *N. fusticula* the inhalant and exhalant siphons (Figure 5) are joined for almost half of their length (Lopes & Narchi, 1998). Most of the specimens have white siphons with small spots of reddish brown pigmentation from the region of separation of the siphons to the aperture. This pigmentation is more abundant on the ventral sides of the inhalant siphon and on the dorsal side of the exhalant.

The inhalant siphon (Figure 6) is fringed with a row of eight digitiform tentacles, between which the epithelium forms simple projections. When the animal is pumping water, the siphons project through the wood, and the digitiform tentacles are kept almost perpendicular to the axis of the siphons.

The exhalant siphon possesses a relatively narrow

opening whereas the margin is smooth and lacks digitiform projections. The exhalant siphon stretches and moves more actively than the inhalant, the latter stayed in the same position for a long period, moving only when disturbed or in order to quickly close the opening by flexing the digitiform projections. This movement apparently occurred without tactile stimulus and was not regular.

The cilia on the siphons (Figure 7) occur mainly on the digitiform projections and the epithelium at the inhalant and the extremity of the exhalant siphons and produce a weak rejecting current that transports small particles outwards. Thus, these cilia contribute to cleaning the tentacle surface, impeding the settling of small particles.

Bankia fimbriatula eliminates fecal pellets and pseudofeces via small jets. The exhalant and inhalant siphons, respectively, eject them a short distance away from the opening in the wood, where generally they accumulate. In the aquarium, large quantities of this waste accumulate, requiring weekly removal.

Musculature of the pallets and siphons

The musculature involved in moving the pallets and siphons (Figure 8) was described by Turner (1966) for *Bankia gouldi* and *B. setacea*. In *B. fimbriatula*, the musculature is similar to that of *B. gouldi* and includes the protractors, anterior retractors, median and posterior retractors and adductor muscles. These muscles unique to the Teredinidae are fixed to the proximal third part of the pallet stalk.

The protactor muscle (pmp) of each pallet is composed of two well-developed bundles, easily seen externally as an open fan shape, with the narrower part directed to the anterior region of the animal. The muscle itself is fixed to the stalk and to the calcareous part of the gallery wall.

The anterior retractor muscle (armp) of pallet is formed by two muscular bundles, the thicker "internal" and the thinner "external." The internal is fixed to the internal face of the stalk and the external is fixed to the external face of the stalk.

The posterior retractor muscle (prmp) is slim with little branching. The posterior retractor muscle ends inside the mantle and is not attached to any hard structure.

The adductor muscle of the pallets (amp), the extremities of which are fixed to the internal face of the stalk, bring together the two pallets.

In the body region where the musculature of the pallets occurs, it is possible to observe two well developed cylindrical muscular bundles of the retractor muscles of the siphon (rms).

When the animal is pumping water, the pallets remain inside the gallery. Any disturbance in the environment causes retraction of the siphons. At this

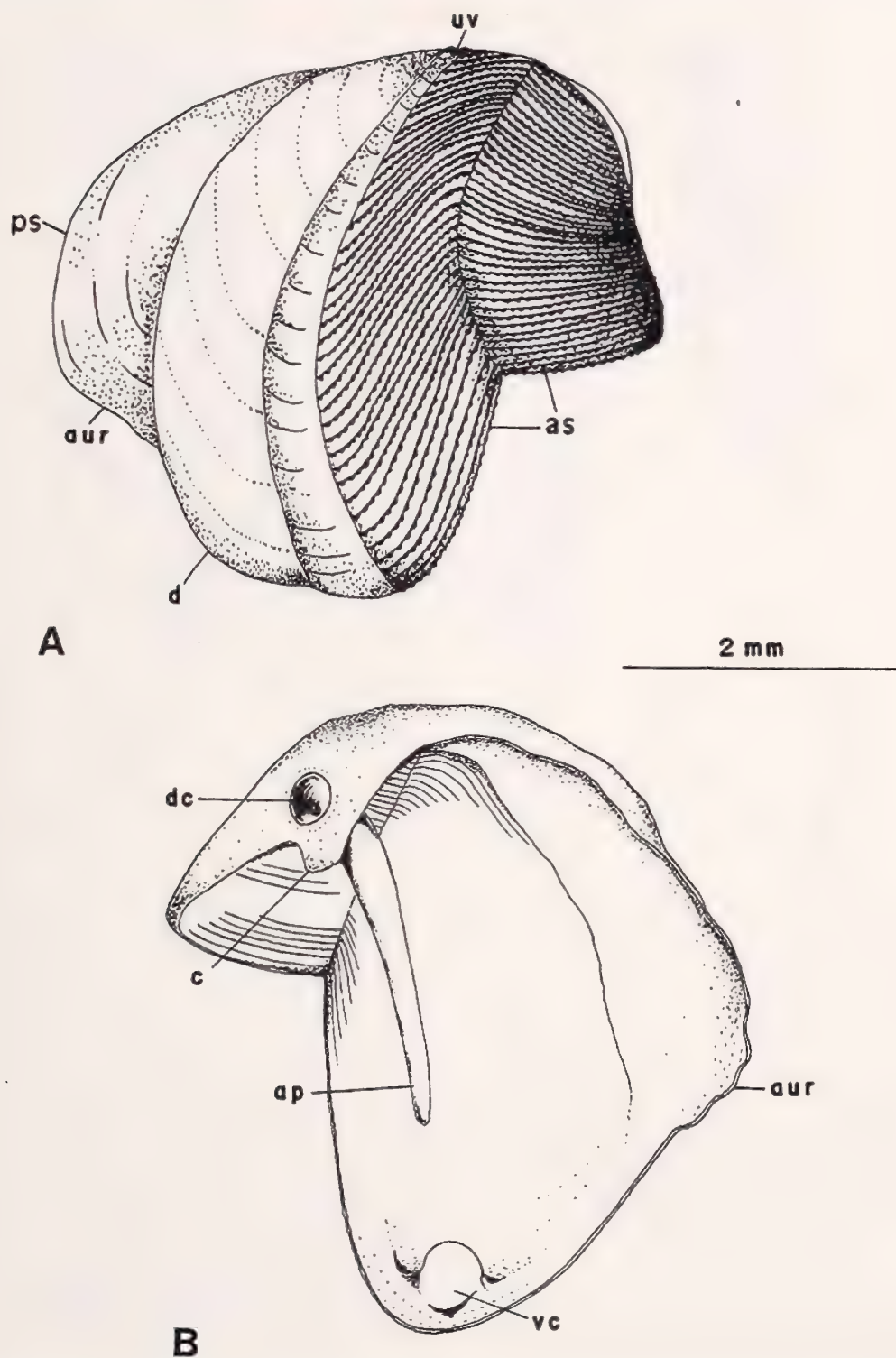


Figure 3. *Bankia fimbriatula*. Right valve of the shell. A. External view. B. Internal view. Abbreviations: ap, apophysis; as, anterior slope; aur, auricle; c, chondrophore; d, disc; dc, dorsal condyle; ps, posterior slope; vc, ventral condyle; vu, ventral umbonal sulcus.

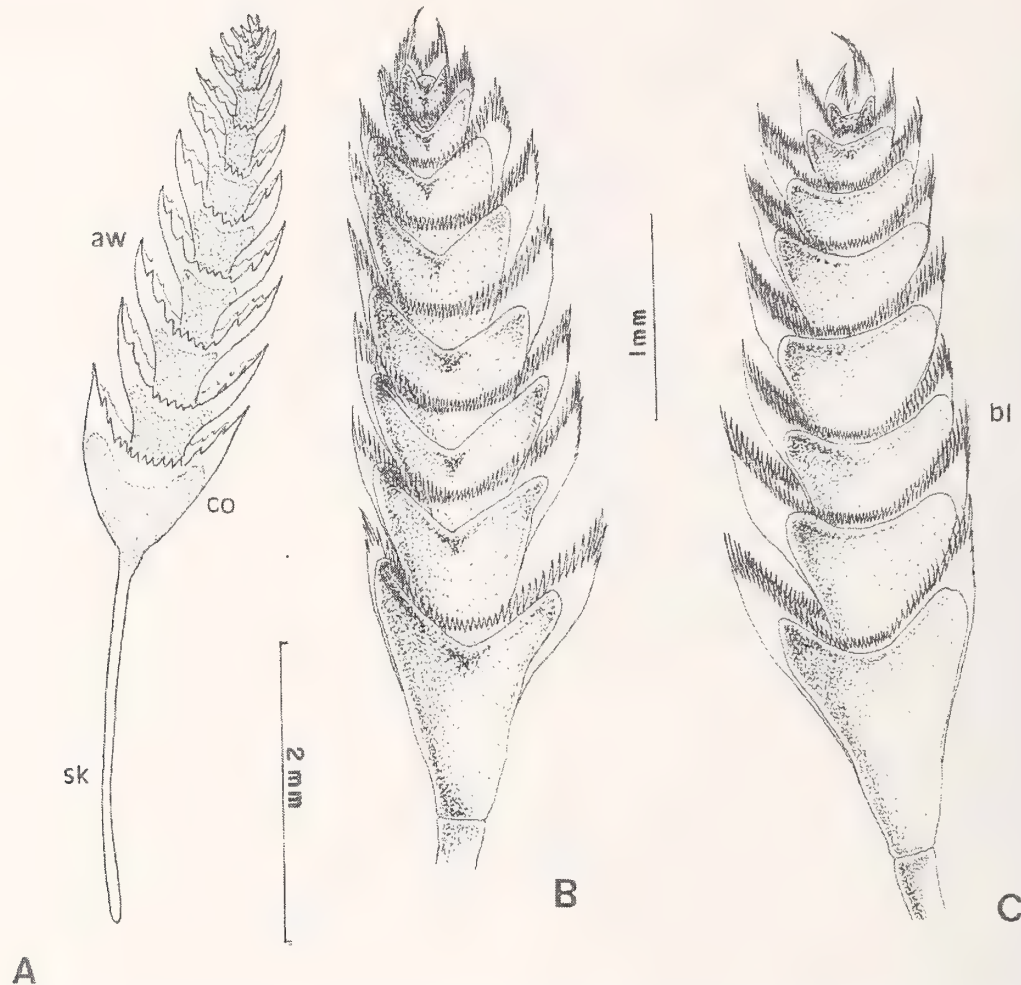


Figure 4. *Bankia fimbriatula*. Variations in the pallet. A. Pallet with complete peduncle. B. External view of the pallet. C. Internal view of the pallet. Abbreviations: aw, awns; bl, blade; co, cone; sk, stalk.

time, the pallets are pushed into the opening of the gallery by contraction of the pallet protractor muscles. When the disturbance ceases, the pallets retract and the siphons extend out to the exterior. Pallet retraction is executed by retractor muscles at the same time that the adductors contract, thus moving the pallets' blades apart, allowing for passage of the siphons. During this process, the protractor muscle of the pallet and the retractors of the siphons remain relaxed.

Mantle

The structure of the mantle is similar throughout the family (Turner, 1966). In *B. fimbriatula* the mantle is thin and transparent in the anterior third of the body. At the median third it is a little thicker, while at the posterior third, it is very thick. The tissue of the mantle is filled with a whitish substance. Groups of round granules of a reddish-brown color, as described by

Lopes & Narchi (1998) in *N. fusticula*, are not present in *B. fimbriatula*.

In the hypobranchial cavity at each side of the body, the internal epithelium of the mantle has a tract with well-developed cilia that extends from the anterior region to the base of the inhalant siphon. In the anterior and median regions of the body, these tracts are lateral. At the beginning of the posterior ctenidia they approach one another, meeting and becoming ventral.

The mantle in the epibranchial cavity dorsal to the posterior ctenidia, near the siphons, has internally a thick zone of mucus cells, as also described by Nair (1957) and Saraswathy & Nair (1971) for *B. carinata*.

Labial palps

The labial palps of *B. fimbriatula* (Figure 9) are attached to the epithelium of the visceral mass (Turner, 1966). They are inconspicuous, the external and the

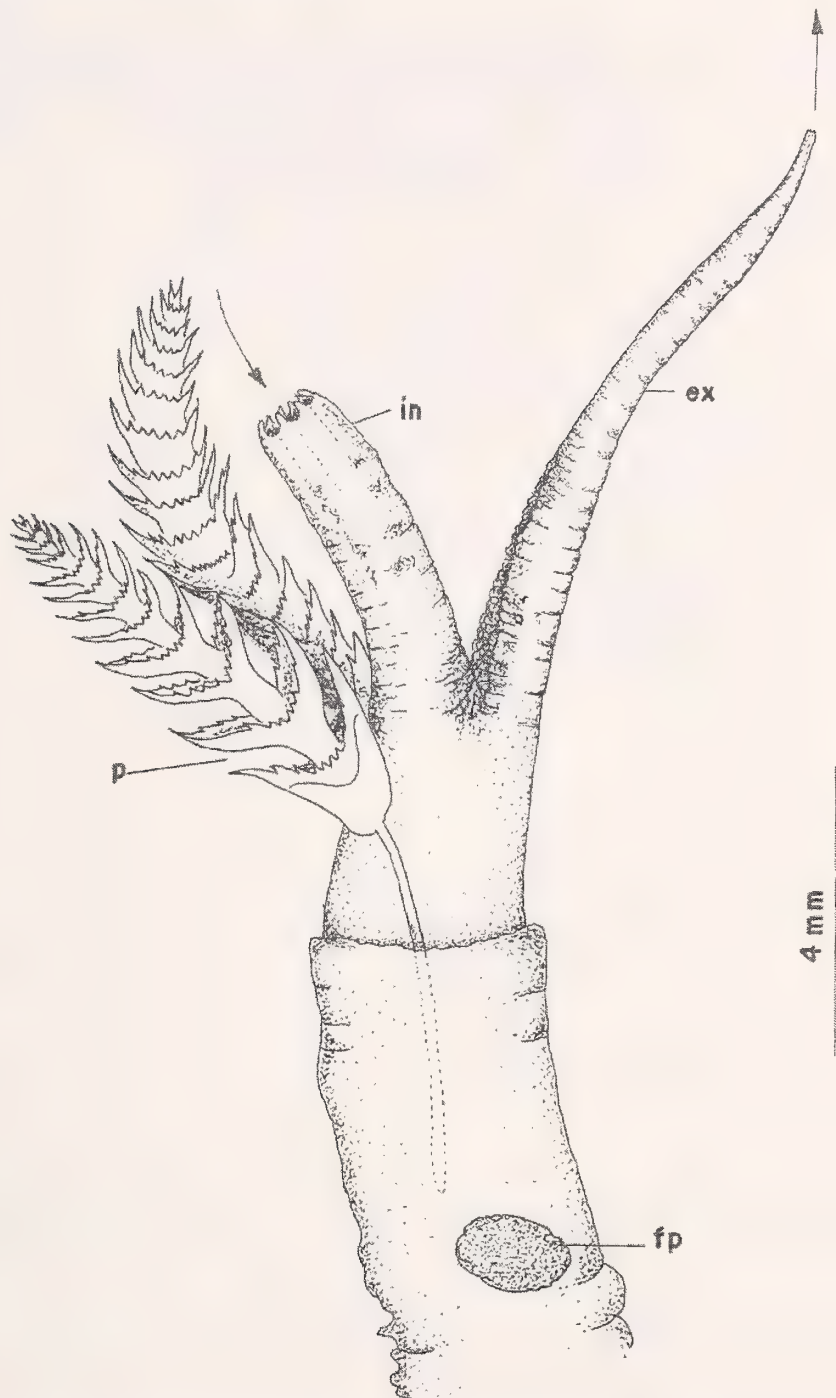


Figure 5. *Bankia fimbriatula*. Siphons and pallets as observed in living animal removed from the wood. Abbreviations: fp, fecal pellet; in, inhalant siphon; ex, exhalant siphon; p, pallet. The arrows show the direction of the inhalant and exhalant currents.

internal ones occupying, respectively, dorsal and a ventral positions. The dorsal palp is reduced to two flat folds. The ventral palp is reduced to a small, long and narrow elevation extending from the ventral border of the mouth to the anterior extremity of the marginal

groove. Identification of the palps was possible only for some specimens.

The ciliary currents were observed only in a few specimens. Ciliary activity was slight and movements of the particles near the mouth were not detected.

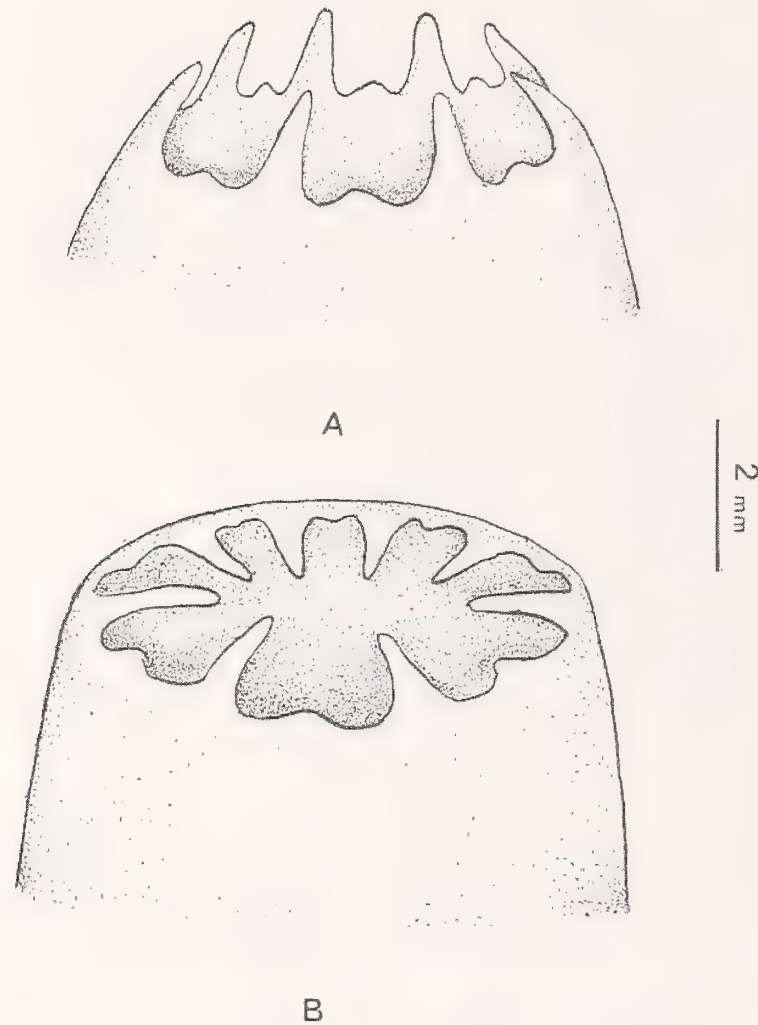


Figure 6. *Bankia fimbriatula*. Detail of the aperture of the inhalant siphon with eight digitiform tentacles. A. Siphon opened with extended tentacles. B. Siphon showing tentacles bending across the aperture.

Ctenidia

The terminology adopted for the description of the ctenidia of *B. fimbriatula* is the same used by Ridewood (1903); Atkins (1937); Purchon (1939) and Lopes & Narchi (1998).

The anterior ctenidia have from eight to nine filaments that correspond to those of the external lamella of the demibranch (Figure 10). Each filament is reduced to a simple bar, joined throughout its length to the epithelium of the visceral mass. The first and the last filaments are really semi-filaments because there is complete ciliation on only one of the lateral faces, as Sigerfoos (1908) described for *B. gouldi*.

Depending on the condition of the body contraction, the ctenidium may become strongly folded, simulating a plait (Figure 11). The body of *B. fimbriatula* can contract to half its length in preserved animals or even

in live ones removed from wood. The posterior part of the body is more affected by this contraction and the ctenidia become shorter and folded. The posterior ctenidia of *B. fimbriatula* are similar to those described by Lopes & Narchi (1998) for *N. fusticula*.

The posterior ctenidia are represented only by the external demibranch [Purchon (1939, 1941) and Lopes & Narchi (1998)].

The demibranchs of *B. fimbriatula* are eulamelli-branch and homorhabdic. Each demibranch has a V-shaped form; the apex possesses a marginal groove 95 μm deep.

Each filament of the posterior ctenidia measures 40.8 μm in width along practically its entire length. The free extremity is slightly dilated. Each filament (Figures 12, 13) has two bands of frontal cilia (fc) laterally disposed, each of which measures around 6.8 μm in length, bordered by two rows of lateral-

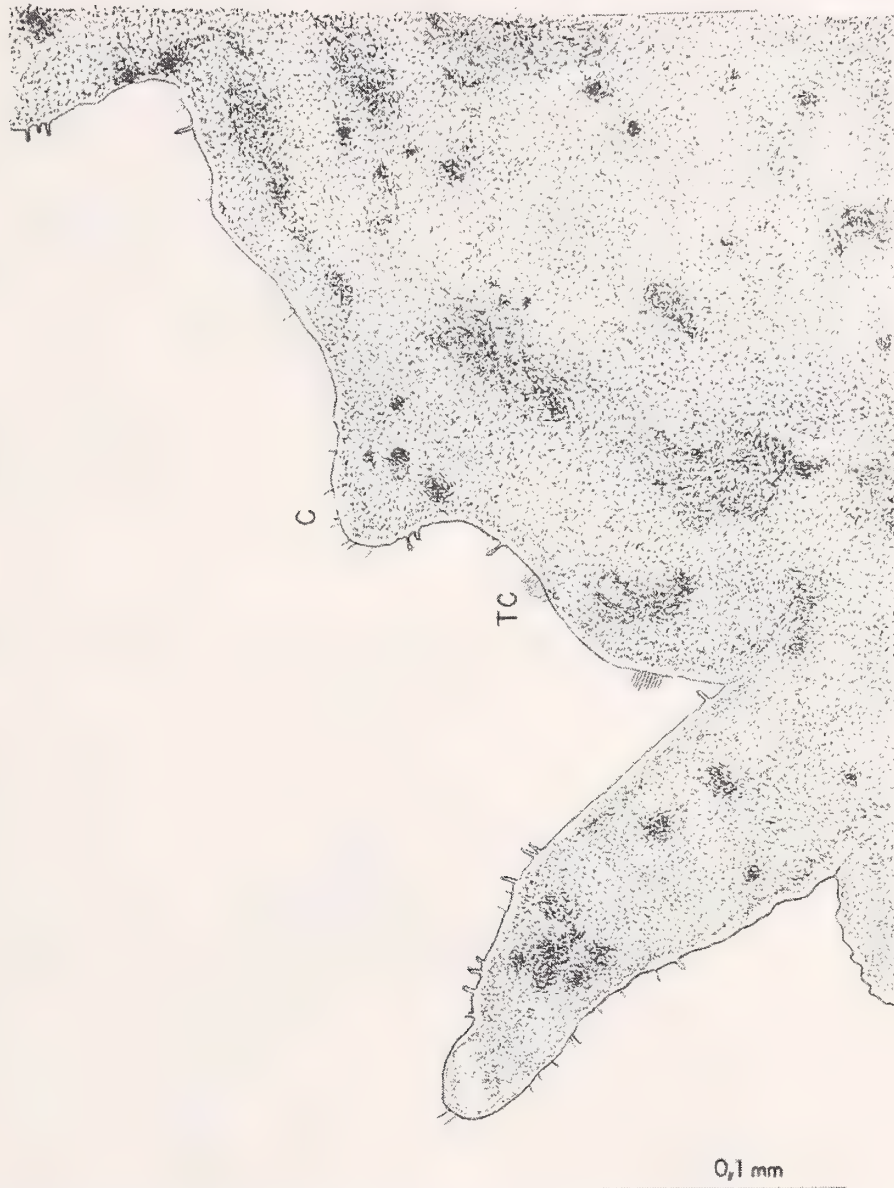


Figure 7. *Bankia fimbriatula*. Rim of the inhalant siphon showing one digitiform tentacle and one simple projection occurring between two tentacles. Abbreviations: c, cilia; tc, cilia tufts.

frontal cilia (lfc) of around $50\text{ }\mu\text{m}$ in length; laterally, between the base of the filament and the lateral-frontal cilia, there are lateral cilia (lc) around $23.8\text{ }\mu\text{m}$ in length forming on each face a strip about $20.4\text{ }\mu\text{m}$ in width. The frontal cilia of the lateral regions of the free extremity of the filaments are the same length and cover the top of the filaments. In this region, there are no large cilia which could be identified as being terminal. The rows of lateral-frontal and frontal cilia end at the marginal groove base and are of similar length as the frontal cilia.

The posterior demibranchs of *B. fimbriatula*, joined

by their respective ctenidial axes, separate at the posterior region of the visceral mass. The filaments become progressively smaller until they are reduced to the marginal groove. This groove is situated laterally on the visceral mass it extends to the anterior ctenidia, and is bordered by ciliated cells.

In the anterior and median regions of the body the ctenidia are reduced to a marginal groove. The quantity of material transported inside the marginal groove is generally small. Excess particles are conducted to the anterior region where they accumulate, surrounded by mucus, and formed into large masses, which flow from

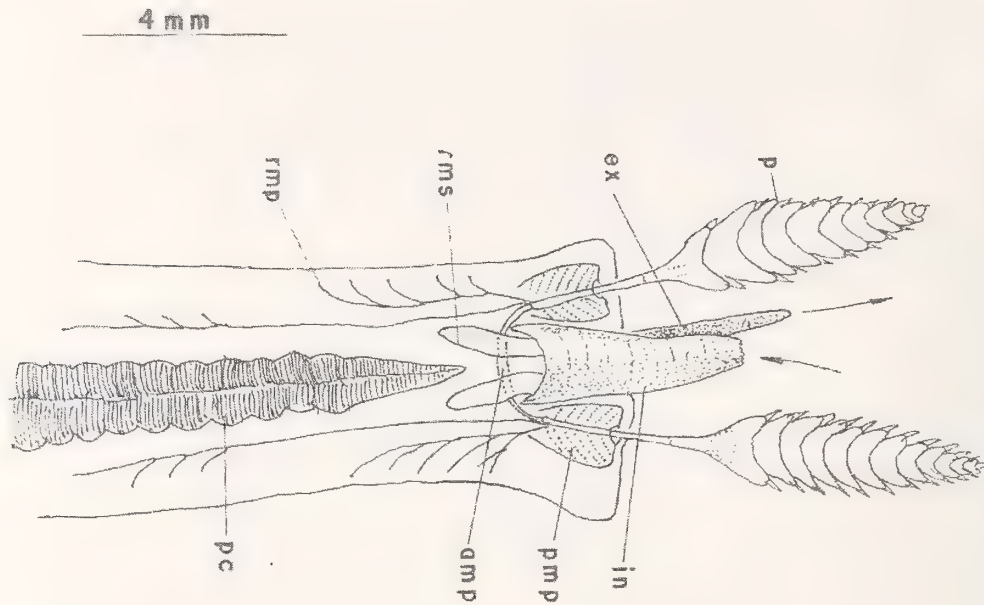


Figure 8. *Bankia fimbriatula*. Diagrammatic view of the muscles associated to the pallets and siphons. Abbreviations: amp, adductor muscle of the pallet; ex, exhalant siphon; in, inhalant siphon; p, pallet; pc, posterior ctenidia; pmp, protractor muscles of the pallet; rms, retractor muscle of the siphon; rmp, retractor muscle of the pallets.

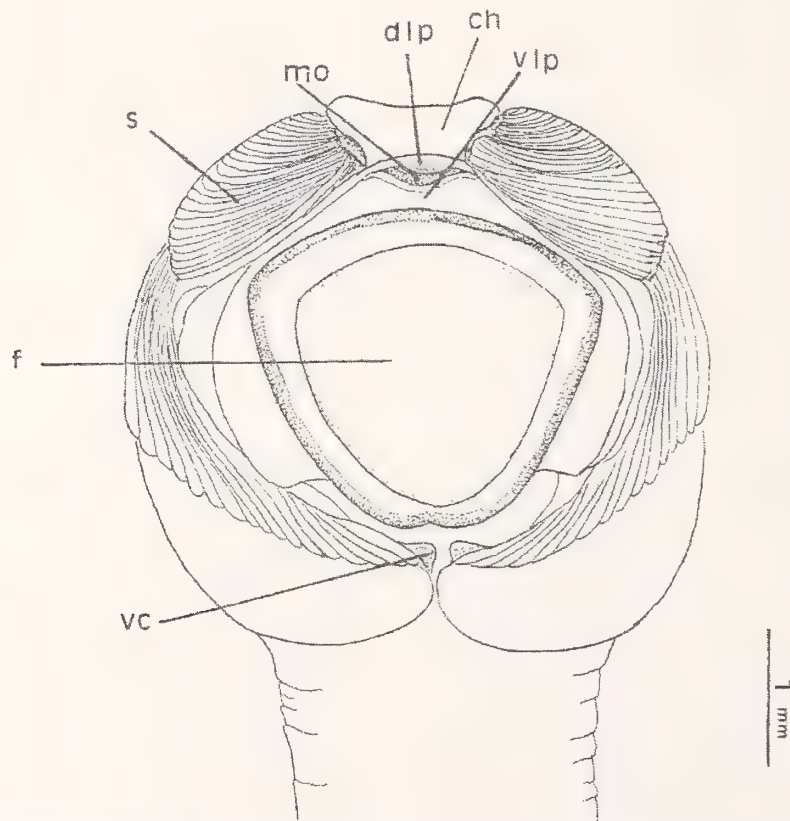


Figure 9. *Bankia fimbriatula*. Frontal view of the anterior extremity. Abbreviations: ch, dorsal hood; dlp, dorsal labial palp; f, foot sole; mo, mouth; s, shell; vc, ventral condyle; vlp, ventral labial palp.

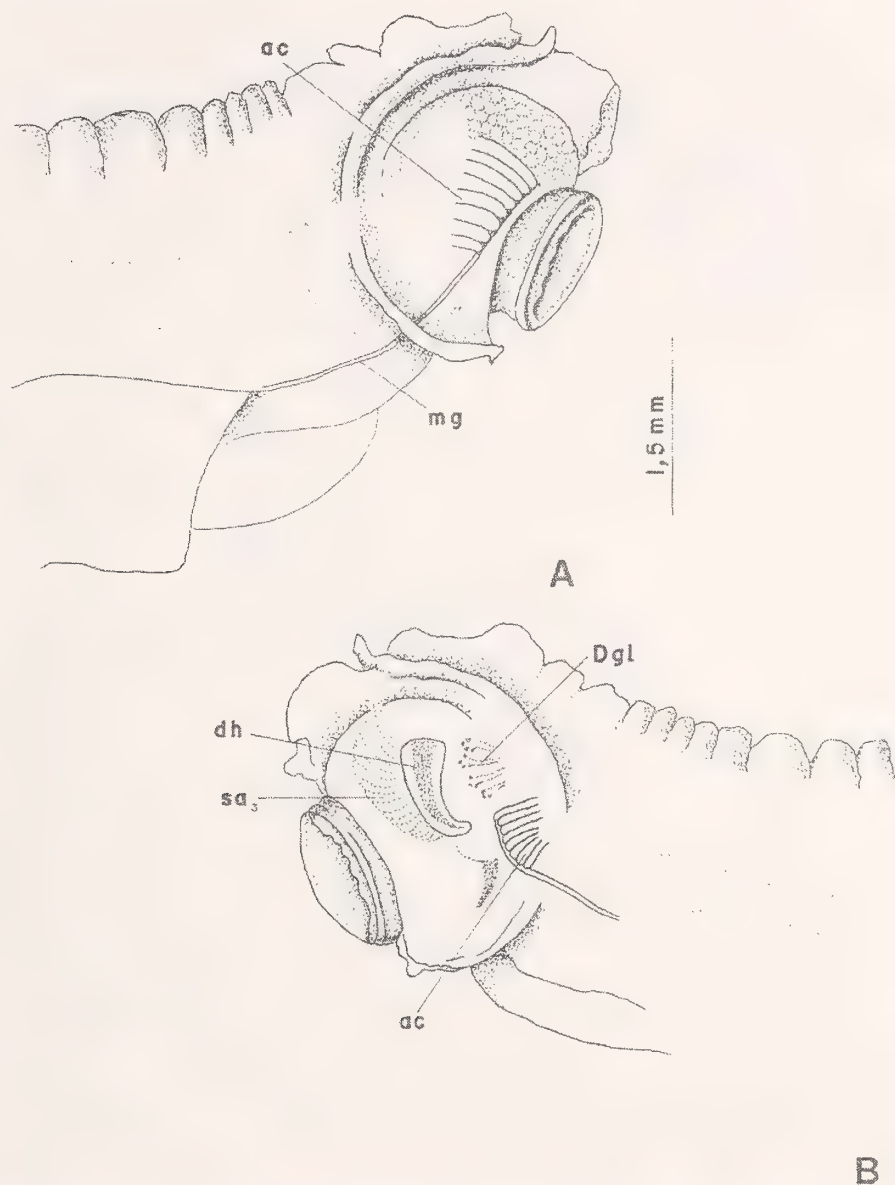


Figure 10. *Bankia fimbriatula*. Topography of the anterior region of the body after removal of the valves and submitted the animal to a process of diaphanization. A. View from the right side. B. View from the left side. Abbreviations: ac, anterior ctenidia; Dgl, Deshayes glands; dh, dorsal hood; mg, marginal groove; sa₃, sorting area sa₃.

inside the groove. These masses are then transported by the cilia of the rejection tract of the mantle and eliminated.

Ciliary Currents

On the filament of each demibranch of the posterior ctenidia, the lateral cilia produce strong water currents, which aid in respiration and feeding. On one face of the filament these cilia produce a ventrally-directed current, and on the other, a dorsally-directed one. The lateral-frontal cilia project toward the sides of the filaments and alternatively cross with the adjacent

filaments to form a type of grating. The lateral cilia beat from the inside out onto the interfilamentar spaces, throwing particles onto the frontal faces of the filament. From here the particles are transported by the two lateral rows of the frontal cilia and large particles are prevented from penetrating in the interior of the demibranchs. The frontal cilia on the external and internal blade of each demibranch conduct particles of different sizes to the ventral region. At the ventral extremity of the filaments, small particles are moved by the cilia from the lateral faces to the interior of the marginal groove and conducted to the

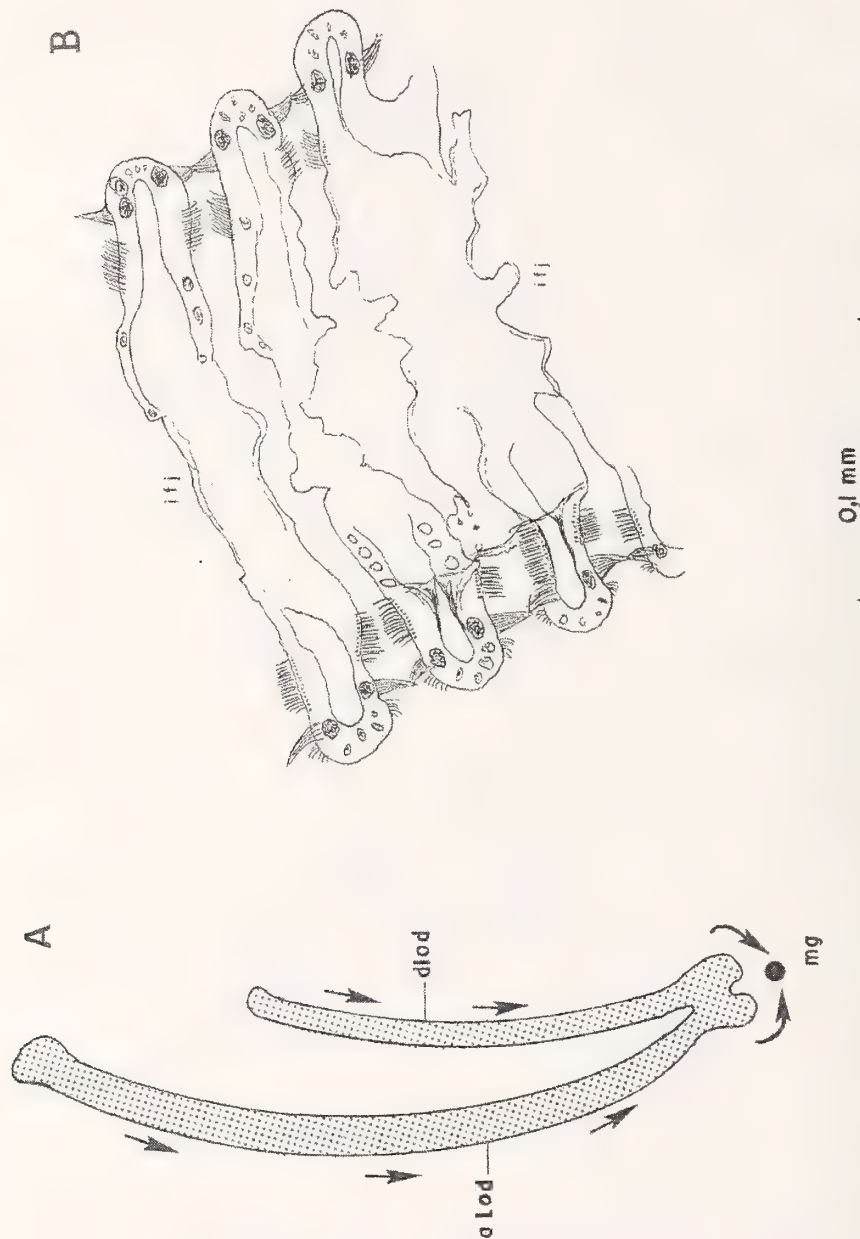


Figure 11. *Bankia fimbriatula*. Posterior ctenidium. A. Diagrammatic vertical section through the ctenidium to show the mode of action of the frontal cilia. B. horizontal section to show the homorhabdic condition of the ctenidium. Abbreviations: alod, ascendent lamella of the outer demibranch; dlod, descendent lamella of the outer demibranch; ifj, interfilamentar junction; mg, marginal groove.

anterior region by a strong ciliary current. Larger particles are conducted anteriorly at the free edge of the demibranch and outside the marginal groove. Opening and closing of the marginal groove were not observed to control the quantities of particles within. Depending on the distance of the marginal groove from the mantle rejection tracts, the strong ciliary currents of these tracts directly captured particles from outside the

marginal groove. Particles that form large masses that fall into the hypobranchial cavity are collected by the rejection tract. These masses are retained by the cilia of the rejection tract of the mantle and then eliminated.

Weak ciliary activity was observed in the mid-region of the visceral mass in a few specimens of *B. fimbriatula*, particles being conducted forward in the marginal groove.

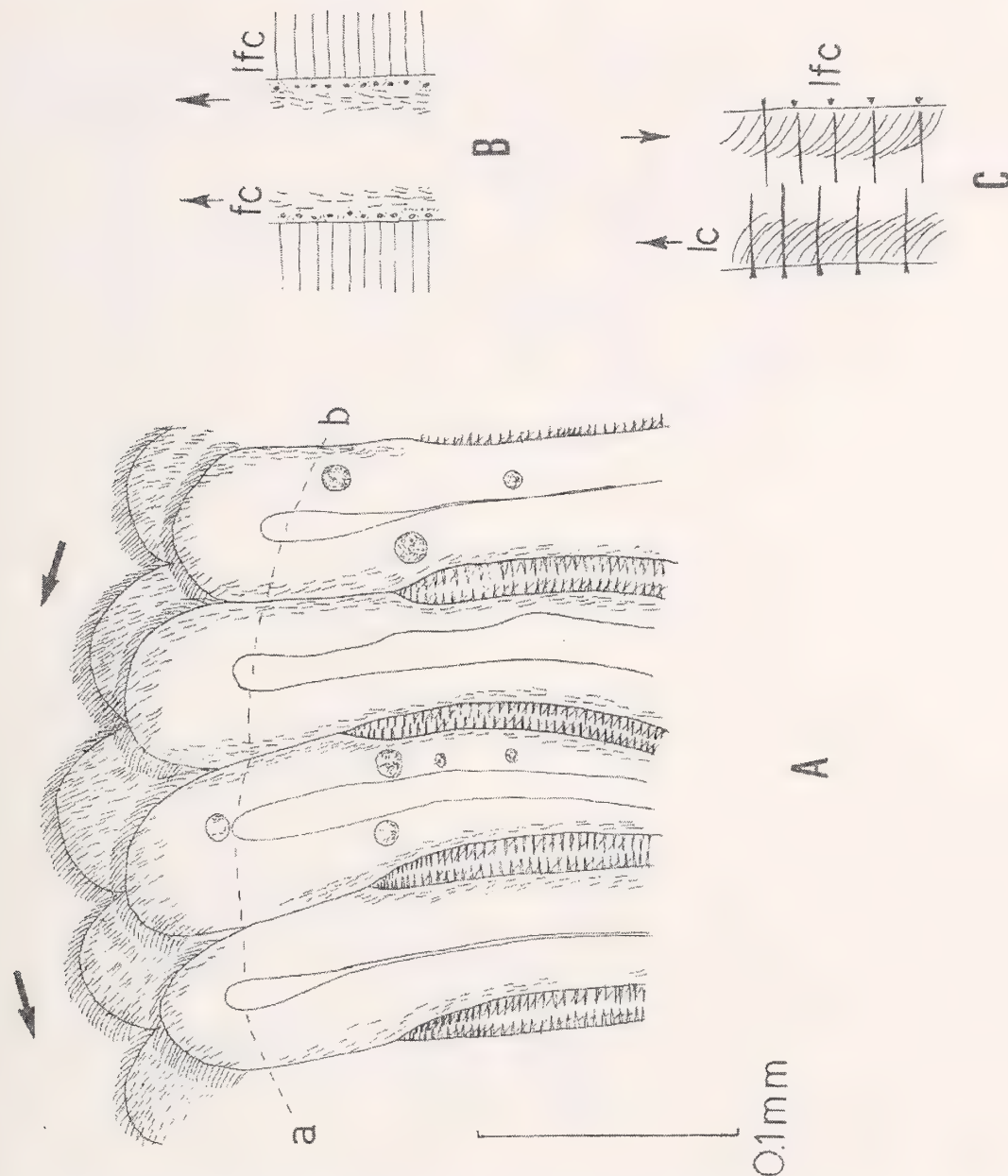


Figure 12. *Bankia fimbriatula*. Marginal groove at the ventral margin of the ctenidium. A. Cilia on the outer surface of the ctenidium; a-b, line of the marginal groove. B. Outer surface of a filament showing the cilia. C. Frontal view between two filaments to show cilia. Abbreviations: fc, frontal cilia; lc, lateral cilia; lfc, latero-frontal cilia; the arrows indicate the direction of ciliary currents, the arrows indicate direction of ciliary currents, including oral one.

The material entering the epibranchial include feces, gametes, excretory products and very small particles which have passed through the demibranchs.

Beside the ciliary currents on the epithelium, frequent contractions were observed throughout the length of the mantle at the epibranchial cavity. The feces were eliminated by short and intermittent jets. No ciliary activity was detected on the wall of the anal canal.

DISCUSSION

The eight simple digitiform tentacles of the inhalant siphon of *B. fimbriatula* and their projection within the inhalant aperture do not act as barriers against particles entering the mantle cavity, but the siphon can regulate the quantity of the material that enters by contracting the circular muscle at the base of the

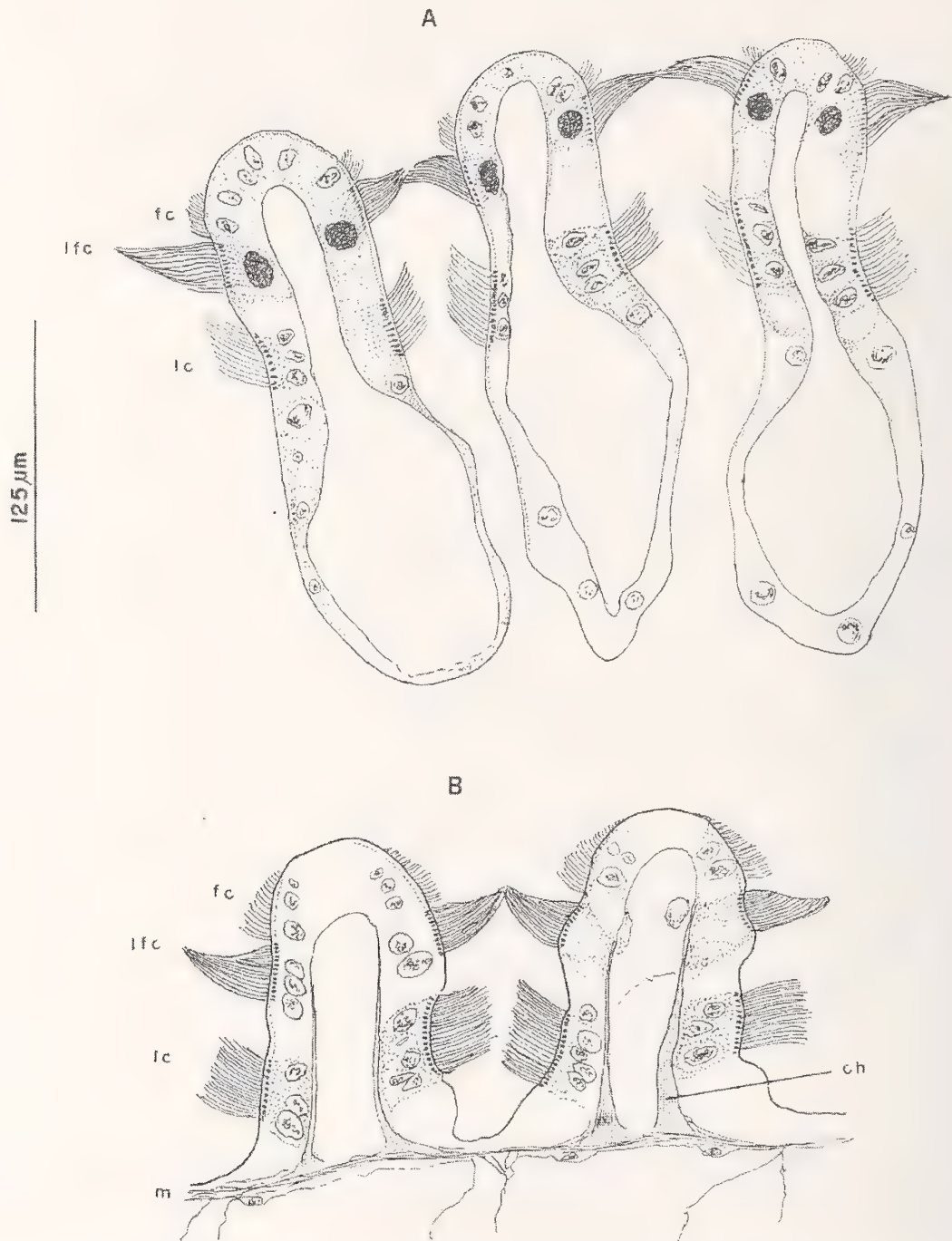


Figure 13. *Bankia fimbriatula*. Transverse sections of the filaments to show cilia. A. Apical filaments. B. Basal filaments. Abbreviations: ch, chitin; fc, frontal cilia; lc, lateral cilia; lfc, latero-frontal cilia; m, horizontal muscles.

tentacle or withdrawing into the interior of the gallery. The ciliary currents of the ctenidia and the efficient rejection tracts of the mantle are responsible for the elimination of rejected particles.

Ciliary activity observed on the tentacles of the inhalant siphon is similar to that described for *N.*

fusticula (Lopes & Narchi, 1998) and is apparently related to the removal of small particles which settle around and accumulate on these structures. The retraction and extension movements of the siphons are probably related to the cleaning mechanism, eliminating larger particles which are not removed by ciliary action.

The exhalant siphon is longer than the inhalant and has no digitiform tentacles at the exhalant opening. The exhalant siphon has great flexibility and shows movements of retraction and extension that can make it increase about three times in length. It has many cilia that remove small particles and it is probably sensitive to mechanical stimuli.

The tentacles of the inhalant siphon were described by Townsley et al. (1965) for *B. setacea* and by Lopes & Narchi (1998) for *N. fusticula*. The tentacles of *B. fimbriatula* are different from those described by Lopes & Narchi (1998).

The sensitivity of the siphons of *B. fimbriatula* to mechanical stimuli, even of low intensity, is similar to that reported for other teredinids (Quatrefages, 1849; Saraswathy & Nair, 1971; Lopes & Narchi, 1998).

The siphons of *B. fimbriatula*, contrary to Turner (1966), are not fairly long and separate, but are united at the basal region for at least one third their length.

The mantle of *B. fimbriatula* is similar to that of other teredinids (Sigerfoos, 1908; Lazier, 1924; Turner, 1966; Saraswathy & Nair, 1971; Rancurel, 1971 and Lopes & Narchi, 1998). A thick mantle is apparently generally distributed throughout the family, especially in older specimens, but is nowhere as great as described in *Kuphus* (Guettard, 1770; Turner, 1966). It has been described for *Bankia* by Bade et al. (1961), Sigerfoos (1908) mentions it for *B. gouldi*; Turner (1966) for *Bactronophorus* Tapparone-Canefri, 1877, *Neoterodo* Bartsch, 1920 and *Nausitora* Wright, 1864 and Lopes & Narchi (1998) for *N. fusticula*. In all species having a thick mantle there were also clusters of red-brown, berry-like structures on the transverse fibers of the middle layers. These structures are not present in *B. fimbriatula*.

The rejection tracts of the mantle in *B. fimbriatula* are separate throughout their length as was observed by Sigerfoos (1908) in *B. gouldi*, by Saraswathy & Nair (1971) in *Nausitora hedleyi* Shepman, 1919 and by Lopes & Narchi (1998) in *N. fusticula*. In *Teredo norvegica* [= *Nototerodo norvegica* (Spengler, 1792)] and *Teredo megotara* [= *Psiloteredo megotara* (Hanley, 1848)], studied by Saraswathy & Nair (1971), these tracts are fused at the posterior body region.

In *B. fimbriatula*, these tracts are fused at the posterior body region on the ventral side up to the basal region of the inhalant siphon.

The anterior ctenidium of *B. fimbriatula* is composed of eight or nine filaments. In *B. gouldi* the number of filaments is usually nine, rarely 10 or 11 (Sigerfoos, 1908). Some authors noted a constant number of filaments: Purchon (1941) recorded ten for *N. norvegica* (= *Nototerodo norvegica*) and seven for *P. megotara*; Saraswathy & Nair (1971), eight for *N. hedleyi* and six for *Teredo furcifera* von Martens, 1894. According to Lazier (1924), there are five filaments in *T. navalis*,

whereas according to Morton (1970), there are eight. Lopes & Narchi (1998) in *N. fusticula* recorded from six to eight filaments, depending on the specimen. This variation is not correlated with the size of the animal.

According to Lopes & Narchi (1998) the absence of variation in filament number or the discrepancy in numbers of filaments in the same species could be related to small sample size.

The posterior ctenidium of *B. fimbriatula* occupies more than 50% of the body length. According to Turner (1966) species with long ctenidia and more developed palps feed mainly on plankton, wood being a less important source to the animal. The appendix of *B. fimbriatula* makes up 1/3 of the body length, showing that wood is an important source of food. The species have a large appendix and the posterior ctenidia are also well developed. This suggests that plankton, as well as wood particles are important in the nutrition of this species.

In *B. fimbriatula*, the basic anatomy of the ctenidia does not significantly differ from that of other teredinid species described by Ridewood (1903), Sigerfoos (1908) and Lopes & Narchi (1998).

In *B. fimbriatula*, however, the fine frontal cilia are laterally disposed in two tracts in the filament, and the central part is free of cilia. Only at the terminal part of the filament, near the marginal groove, fine cilia cover the entire marginal tip of the filament.

Comparing the anatomical characters described in the present work for *B. fimbriatula* with those of *B. gouldi* described by Sigerfoos (1908), Clapp (1951), Turner (1966) and Tan et al. (1993) we conclude that *B. fimbriatula* differs from *B. gouldi* in terms of the pallets, the presence of eight tentacles around the inhalant siphon and the deep marginal groove in the posterior ctenidium. *Bankia fimbriatula* differs also from *B. gouldi*, *B. setacea*, *B. campanellata* and *B. australis* by the presence of tubular auricles intensively pigmented (Turner, 1966). In addition, *B. fimbriatula* differs from *B. carinata* studied by Bade et al. (1961) and Saraswathy & Nair (1971) in the position of the gonads and the large size of the appendix and the great development of the posterior ctenidia.

According to Turner (1966) the variation exhibited by dissected individuals is considerable. Within the range of the genus much more additional work will be necessary before the many subgenera described on the basis of the pallets can be evaluated.

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excellent mollusc researcher and his papers, published in major international journals, made the study of bivalve anatomy easy to carry out. Thank you Dr Walter very much for being my mentor.

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Drilling Localization on Bivalve Prey by *Octopus rubescens* Berry, 1953 (Cephalopoda: Octopodidae)

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One Sentence Abstract. An examination of 171 shells of clams (*Venerupis philippinarum* (Adams & Reeve, 1850)) eaten by *Octopus rubescens* Berry, 1953 showed that holes in them were drilled by the octopuses preferentially (64.3%) in adductor muscle scar areas (anterior or posterior), which together comprised only 6% of the total shell area.

Key Words: octopus, drill holes, bivalves, adductor muscles.

Octopuses are well-known generalist predators (Hanlon & Messenger, 1996), but within this generalist approach they also display individual dietary preferences (Anderson & Mather, 2007) and feeding methods (Dodge & Scheel, 1999). Bivalves make up a substantial part of the diet of many octopuses and the methods octopuses use when drilling them, while time-consuming (Steer & Semmens, 2003), are not well-documented and appear to be highly variable (Anderson & Mather, 2007). After drilling, octopuses inject venom into clam prey in order to paralyze the muscle (Nixon & Maconnachie, 1988). Such energy expenditure in drilling might be minimized by selection of particular locations on the bivalve shell (Steer & Semmens, 2003). Anderson & Mather (2007) reported that *Enteroctopus dofleini* drills clams in the center of the shell. This is unlike *O. vulgaris*, which drills around the edge (Ambrose & Nelson, 1983), and *O. dierythraeus* (Norman, 1993, *O. minus* Gould, 1852 or *O. bimaculoides* Pickford & MacConnaughey, 1949, which drill over the adductor muscles (Steer & Semmens, 2003; Cortez, et al., 1998; Casey, 1999, respectively).

This inter-specific variation in drilling behavior highlights the fact that one of the central problems octopuses face when feeding on bivalves, in addition to choice of prey, is where to drill on a clam's shell, as different areas of the shell may be thicker or thinner and vital organs of the clam are located in species-specific areas (Kozloff, 1990). Observations of clams eaten by *O. rubescens* at the Seattle Aquarium indicated that individuals may learn to drill clams in particular locations (Anderson, et al., in prep.), while drilling efficiency appears to deteriorate during senescence (Anderson et al., 2008). Despite these observations on

potential life-stage specific differences, there are no detailed studies of the localization of drill holes by mature *O. rubescens*, and that is the subject of this report.

Ten *Octopus rubescens* (mean weight: 73.2 g; SD = 64.6) caught in the wild were held at the Seattle Aquarium and fed only Manila clams (*Venerupis philippinarum*, (Adams & Reeve, 1850)) obtained from a local fish market. At least ten shells from clams that had been drilled and eaten were then collected from each octopus over a period of a month (n = 171; an additional 187 were eaten but undrilled). All drilled shells had one hole in them. The holes were typically 1.4 mm wide on the surface (n = 30; SD = 0.28) and 0.4 mm wide on the inner surface of the shell (n = 30; SD = 0.15) as measured with a light microscope. The dimensions of the eaten shells and their adductor muscle scars were also measured and their areas calculated ($\pi \times L \times W/2$).

Locations of drill holes in shells were classified as occurring in the umbo, center, posterior, anterior, or ventral regions of a shell, by the methods of Anderson & Mather (2007) (see Figure 1) and further, whether they occurred within an adductor muscle scar. The mean shell length was 36.2 mm (SD = 4.57). The mean area of the anterior adductor muscle was 2.6% of the shell area and the posterior muscle scar was 3.7% (n = 171).

We used a replicated test of goodness-of-fit (Sokal & Rohlf, 1995) to determine whether proportions of drill hole location (umbo, center, posterior, anterior, or ventral) differed significantly from 20:20:20:20:20. A significant result in the first analysis would indicate non-random targeting of particular areas of the shells. We again used a replicated goodness-of-fit test to

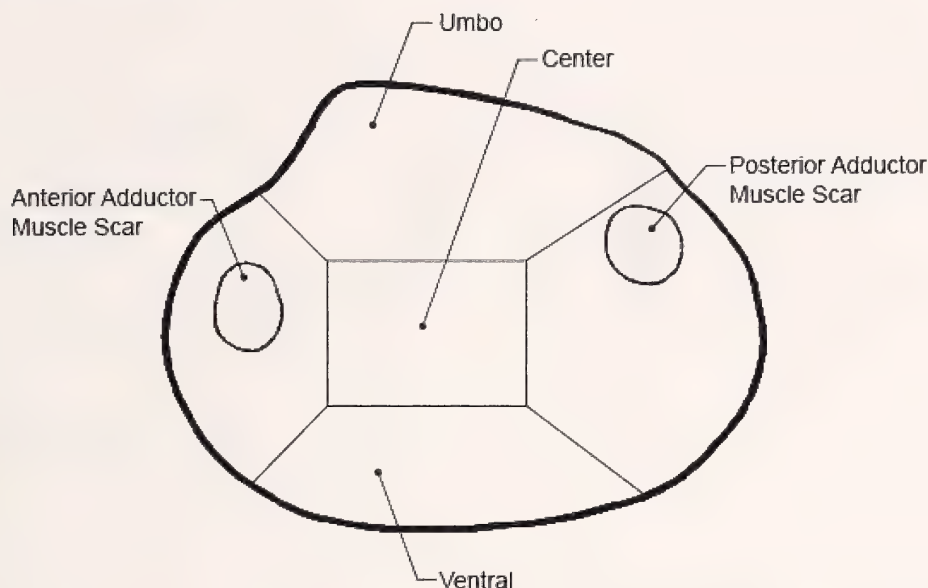


Figure 1. Typical clam shell (*Venerupis philippinarum*) drilled by *Octopus rubescens*. The mean shell length was 36.2 mm. The mean area of the anterior adductor muscle was 2.6% that of the whole and the posterior muscle scar was 3.7% ($n = 171$). The areas are stylized but are roughly equal in area.

determine whether drill hole location (over adductor muscles or outside adductor muscles) differed from the expected frequency of 6:94. A significant result in the second analyses would indicate that octopuses were actively targeting adductor muscles. Since octopuses could contribute to more than one observation in both analyses we first tested whether the outcomes of all the octopuses were homogeneous (i.e., heterogeneity G -test), that is, were individuals uniform with respect to frequencies of drill holes in the different regions of shell. After taking this octopus individuality into account, we then tested whether the sample as a whole fit the expected ratio of frequencies (i.e., results were pooled within each octopus: total G test). This approach allowed us to examine both individual-level as well as overall average pattern of drilling localization.

Two of 10 individual octopuses drilled with equal probability in each of the five valve locations (heterogeneity G -test = 100.85, $df = 36$, $P < 0.05$) but overall, there was still a clear significant preference for octopuses to drill in anterior regions of the clams (total G -test = 213.35, $df = 40$, $P < 0.05$). It was also clear

that octopuses were targeting the adductor muscle scars: 64.3% of drill holes were in adductor muscle scars (anterior or posterior), which together comprised only 6% of the shell area. Once again, while some individuals did not drill over muscles as frequently as others (heterogeneity G -test = 40.15, $df = 8$, $P < 0.05$), there was still a strong significant overall trend for octopuses to drill within muscle scar areas (total G -test = 445.78, $df = 10$, $P < 0.001$).

Although there are slight differences between external features of the anterior and posterior ends of *Venerupis philippinarum* (e.g., the anterior end is very slightly pointed and the posterior end is rounded, see: Coan et al., 2000), it is interesting to note that the majority of octopus drill holes were located in the anterior end (52% of all observed drill holes, 20% expected by chance alone) and that most individuals appeared to target the adductor muscles. *Octopus rubescens* is known for its potent venom (Hanlon & Messenger, 1996) so targeting adductor muscles which hold the clam shells closed (Kozloff, 1990) for venom injection and paralyzing one of the adductor muscles

Table 1

Frequencies of drill hole locations found in different regions of clam shells left after predation by *Octopus rubescens* ($n = 171$).

	Anterior	Posterior	Umbo	Center	Ventral	Within muscle scar
Total N	89	24	34	18	5	110
Percentage	52.0	14.0	20.5	10.5	2.9	64.3

may be the most efficient means of accessing food. Cortez et al. (1998) hypothesize there may a direct effect on the nervous system of the clam by injecting venom in any anterior region of the clam. This brings up the interesting question of what features (physical and/or chemical) of clam shells octopuses use to gather information regarding internal location of clam organs and musculature. Given that half of the clams eaten during our study were not drilled at all, are these same cues used to determine whether to drill at all? Clearly, further studies are needed to ascertain the conditions which favor *non*-random drilling behavior in octopuses, including the apparent efficiency of octopuses at drilling shells from clam species with short co-existence histories and the maintenance of behavioral individuality and foraging strategies witnessed here and in other studies (Mather & Anderson, 1993; Sinn et al., 2001).

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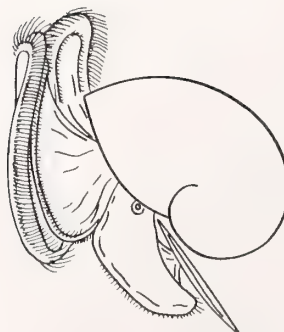
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ROLAND C. ANDERSON, DAVID L. SINN AND JENNIFER A. MATHER 326



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